Effects of soil nutrient availability on non-native invasive and native plants in Hawaiian wet and dry ecosystems

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERISTY OF HAWAIʻI AT MĀNOA IN PATIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTERS OF SCIENCE
IN
NATURAL RESOURCES & ENVIRONMENTAL MANAGEMENT
(ECOLOGY, EVOLUTION AND CONSERVATION BIOLOGY)

December 2016

By
Amanda Knauf

Thesis Committee:

Creighton M. Litton, Chairperson
Rebecca J. Cole
Christian P. Giardina
Jed P. Sparks

Keywords: carbon amendments, invasive species, resource use strategy, restoration, tropical ecosystem

Acknowledgments

Funding for this research was provided by the Department of Defense Strategic Environmental Research and Development Program (RC-2433), the USDA Forest Service Institute of Pacific Islands Forestry, and the College of Tropical Agriculture and Human Resources at the University of Hawai'i at Mānoa via the USDA-NIFA McIntire-Stennis program (HAW01123M).

I thank my committee chair Dr. Creighton Litton for his constant guidance, advice during experiment setup, help with data collection and analysis, and thorough edits and comments throughout the writing process. I also extend my thanks to committee member Dr. Rebecca Cole for all her assistance in Hilo with the project setup, maintenance, and completion, and for her continuous assistance with data analysis, public presentations, and thesis comments. In addition, I thank committee member Dr. Jed Sparks for all his assistance with ecophysiological research, assistance with gas exchange measurements, and thesis comments. I thank my final committee member, Dr. Christian Giardina, for his assistance with the US Forest Service facilities and thesis comments. I would also like to acknowledge Dr. Ken Gerow of the University of Wyoming for assisting me with the statistical data analyses, for which I am very grateful.

I thank the technicians, interns, and volunteers for their assistance in data collection and plant processing: Kim Sparks, Malia Stewart, Rob Hamnett, Taylor Tomita, Cyra Macanas, Melanie Quiñones , Kylle Roy, Eva Brill, Alex Kleymann, Bradley Kaufmann and Riley De Mattos.

I thank my lab mates and fellow NREM graduate students for their continued support and encouragement. I'd like to especially thank Becky Ingram and Matt Lucas for talking through all aspects of my research and for keeping me sane. Finally I'd like to thank my family and friends for their continual support. Love to my mom for sending me the best care packages and to my dad for always helping me through my car issues. And to my brother and sister, thank you for visiting and making me do fun things.

Abstract

Native ecosystems globally face constant pressure from nonnative, invasive plants. One potential restoration technique to favor native species is to decrease soil nutrient availability via carbon amendments. I evaluated survival, growth, reproductive output, resource use efficiency (RUE) and ecophysiology of native and invasive species from Hawaii in a greenhouse experiment in each of five soil nutrient treatments. Results show that, in general, native species had neutral responses to soil nutrient levels, whereas large decreases in growth and whole plant carbon gain of invasive species were observed with decreasing soil nutrients. Photosynthetic capacity was constant for all species across varying soil nutrient levels. RUE of native species was constant, while that of invasive species decreased with decreasing soil nutrient availability. Collectively, these results suggest that reducing soil nutrient availability is a promising technique for restoring native Hawaiian ecosystems where nutrient availability is high and invasive species are a concern.

Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

Non-native invasive species are so widespread that they are considered a large component of global environmental change, posing a serious problem for the conservation, restoration and management of terrestrial ecosystems globally. Invasive species can alter biological diversity, ecosystem processes, and the physical environment in ways that promote further invasion and reduce ecosystem services (Vitousek et al. 1996). As a result, management strategies to control the negative impacts of invasive species are increasingly needed. Understanding competitive dynamics between native and invasive species provides key information for successfully managing invasive species to restore native communities and ecological processes.

An important area where research can potentially inform management lies in understanding how resource availability and resource use efficiency impact competition between non-native invasive and native species. Prior research has shown that reducing soil nutrient availability (e.g., with carbon amendments) can reduce the abundance of non-native invasive species and potentially tip the competitive balance to favor native species, particularly in systems adapted to low resource availability (Alpert and Maron 2000, Blumenthal et al. 2003, Alpert 2010). Conversely, increased soil nutrient availability, which is commonly observed in disturbed environments, typically favors non-native invasive species (Ostertag and Verville 2002b, Blumenthal et al. 2003). However, the effect of soil nutrient availability on competitive dynamics between non-native invasive and native plants in tropical systems is largely untested, particularly for woody species (Alpert 2010). A better understanding of how non-native vs. native competitive dynamics are affected by soil nutrient availability in tropical ecosystems will inform restoration and conservation by providing land managers with tools that can be applied in target management areas.

Resource Use Efficiency (RUE) of native and invasive species

Several physiological and morphological plant traits are related to growth and resource use efficiency (RUE; carbon assimilation per unit of resource). These traits include photosynthetic rates (A), internal leaf CO_2 concentrations (C_i), stomatal conductance (g_s), specific leaf area (SLA, leaf area per unit leaf mass), and leaf nutrient concentration. In

general, higher *A* leads to higher rates of biomass accumulation and growth (Lambers and Poorter 1992). Rates of *A* are related to C_i, and A/C_i curves can be used to determine carboxylation capacity (V_{cmax}) and the chloroplast electron transport capacity (J_{max}), both indices that describe the maximum rate of energy acquisition and carbon fixation that a given plant may achieve. Specific leaf area is key to plant growth and efficiency, and typically is positively related to photosynthetic rates (Lambers and Poorter 1992, Reich et al. 1997). Leaf nutrient (i.e. N and P) concentrations are typically associated with RUE, where plants with low levels of foliar nutrients typically have higher nutrient use efficiency (Chapin 1980). In turn, lower nutrient use efficiency is typical in species with higher leaf nutrient concentrations, especially N, which promotes fast growth such as that typically seen in invasive species (Field and Mooney 1986).

The successful invasion of a non-native species is often context dependent, and no species is a superior competitor in every environment (Daehler 2003). Functional traits commonly associated with invasive species success include high relative growth rates (Burns 2004, Garcia-Serrano et al. 2005, Burns 2006, Gurevitch et al. 2008), low leaf mass per unit area (Pammenter et al. 1986, Durand and Goldstein 2001, Grotkopp and Rejmánek 2007), and high photosynthetic rates (Baruch and Goldstein 1999, McDowell 2002, Funk and Vitousek 2007). These traits are all indicative of a resource exploitative strategy, which is congruent with the observation that invasive species typically invade areas of high resource availability, such as that occurring after a disturbance (Burke and Grime 1996, Daehler 2003). Native species, in contrast, are often more adapted to low resource availability and typically have traits associated with a resource conservation strategy that includes high resource use efficiency.

Although invasive species are well known for invading areas of high resource availability, they have also been observed invading areas of low resource availability where they display functional differences compared to native species. (Funk and Vitousek 2007, Matzek 2011, Heberling and Fridley 2016). Differences in the mechanisms involved in the uptake and use of nutrients between nutrient-poor and nutrient-rich environments can at least partially explain invasive species success at low nutrient availabilities. In low nutrient environments, most studies show successful invasive species to have resource conservation strategies including: high nutrient-use efficiency (Funk and Vitousek 2007,

González et al. 2010, Matzek 2011), high resistance to low nutrient levels (Schumacher et al. 2009), long nutrient residence times (Laungani and Knops 2009), and high trait plasticity (González et al. 2010).

To date, the majority of studies that have examined RUE and associated traits in native vs. non-native invasive plants suggest that invasive species are successful, at least in part, because of resource exploitative strategies. A meta-analysis by Van Kleunen et al. (2010) found that invasive species had higher values of performance related traits associated with plant physiology and growth rates. A number of studies support this meta-analysis by finding that invasive species typically have higher rates of photosynthesis (Pattison et al. 1998, Baruch and Goldstein 1999, Funk and Vitousek 2007, Peñuelas et al. 2010, Matzek 2011), nitrogen use efficiency (Baruch and Goldstein 1999, McDowell 2002, Matzek 2011), leaf nitrogen content (Baruch and Goldstein 1999, Peñuelas et al. 2010), and specific leaf area (Baruch and Goldstein 1999). Conversely, studies examining invasive species in low resource environments have found that invasive species can also have traits of resource conservation (Funk and Vitousek 2007, Matzek 2011). Not all species display the same traits, however, and it is unclear how the performance of invasive species with resource exploitative strategies are impacted by varying nutrient conditions when in competition with native species adapted to low resource availability (McDowell 2002, Funk and Vitousek 2007, Matzek 2011).

Soil nutrient manipulation as a restoration management tool

In systems where native plants are adapted to low resource availability, such as in the Hawaiian Islands, decreased soil nutrient availability could potentially help counter invasion by non-native species by altering competitive dynamics to facilitate native species (Blumenthal et al. 2003, Burke et al. 2013). One method of soil nutrient reduction is to promote the uptake of available inorganic nitrogen by soil microbes by amending the soil with a metabolic substrate that is high in carbon and low in nutrients (e.g., a high C:N), such as sucrose, cellulose, lignin, or sawdust (Alpert 2010). Soil microbes use both the carbon and nitrogen in these substrates to maintain a C:N ratio of ~8:1. As a result, when a substrate with a high C:N is added to the soil, the demand for nitrogen by soil microbes will be greater than the nitrogen content of the residue they are utilizing, resulting in

immobilization of inorganic nitrogen (NH_4^+ and NO_3^-) in microbial biomass from the surrounding soil solution, and a subsequent reduction in the availability of soil nutrients to plants.

Globally, prior studies have shown that carbon amendments can be an effective approach to stimulate microbial nitrogen immobilization and reduce soil nitrogen availability (Gallardo and Schlesinger 1995, Schaeffer et al. 2003, Alpert 2010, Perry et al. 2010, Burke et al. 2013). However, the effects of nutrient immobilization on native vs. non-native species have been mixed. In the most successful studies, carbon additions have resulted in an increase in native biomass and decrease in non-native biomass (Allen and Zink 1998, Blumenthal et al. 2003, Perry et al. 2004, Prober et al. 2005a, Prober et al. 2005b, Eschen et al. 2007). Importantly, these studies have shown that carbon amendments favor native species in one of two ways: (*i*) by reducing non-native invasive species while having no effect on native species (Horn and Redente 1998, Alpert and Maron 2000, Paschke et al. 2000); or (*ii*) by reducing invasive species growth more than native species growth (Eschen et al. 2006, Bleier and Jackson 2007, Blumenthal 2009). However, other studies have shown that carbon additions may reduce native species growth as much or more than non-native, invasive species (Morghan and Seastedt 1999, Monaco et al. 2003, Suding et al. 2004, Gendron and Wilson 2007). Further, some studies have found that decreased nutrient availability via carbon amendments had no effect on either native or non-native species (Paschke et al. 2000, Cione et al. 2002, Corbin and D'Antonio 2004). Differences in the responses of native and non-native species to reduced soil nutrient availability across studies may be related to the physiology of the plants and general site resource availability. To my knowledge, only one study has looked at both soil nutrient reduction via carbon amendments and subsequent effects on plant physiological traits (Steers et al. 2011). In this prior study, native and invasive species did not differ in their nitrogen use traits and, therefore, soil nutrient reduction did not affect plant abundance measures differently for native and invasive species. However, differences were present in water use efficiency (WUE) where invasive species were found to be more susceptible to drought. Although the use of carbon amendments to reduce soil nutrients in this study was not an optimal restoration tool, it did demonstrate how linking plant physiological responses to resource availability could inform restoration with the use of carbon

amendments. These authors went on to state that the use of carbon amendments is most likely to be successful in situations were the nonnative, invasive species differs strongly in nitrogen use traits compared to native species (Steers et al. 2011). The effect of carbon amendments on native vs. non-native invasive species in tropical systems and, in general, with woody species have received very little attention to date (Alpert 2010). Given the mixed results across disparate systems, the viability of this restoration technique in the tropics and/or for woody species is entirely unknown.

Invasive Species in Island Ecosystems

Invasive species are more likely to negatively impact resident plant and animal communities on islands compared to mainland ecosystems (Pyšek et al. 2012). This is particularly true for small and isolated islands such as the Hawaiian Islands, which have very low resistance to invasion (Carlquist 1974, Denslow 2003, O'Dowd et al. 2003, Gimeno et al. 2006). Invasive species, especially those with characteristics novel to the invaded ecosystem (e.g., nitrogen fixation), typically outcompete native species for resources but can also alter ecosystem processes in ways that make it more difficult for native species to persist (Vitousek 1986, Vitousek and Walker 1989, Vitousek 1990, D'Antonio 2000). In addition, the establishment of non-native invasive plants is often facilitated by a disturbance event (e.g., wildfire or herbivory by non-native ungulates) that increases resource availability (Davis et al. 2000).

Non-native ungulates impact native ecosystems both directly via herbivory and trampling, and indirectly via changes to ecosystem processes that at least partially determine resource availability. In tropical and temperate ecosystems, feral goats, sheep, and pigs can substantially increase the area of exposed soil and subsequently enhance soil erosion rates (Scowcroft and Hobdy 1987, Anderson and Stone 1993, Siemann et al. 2009, Cole and Litton 2014). Additionally, these animals can have major impacts on plant community structure through selective herbivory and alteration of competitive dynamics between native and non-native plants (Cushman et al. 2004, Oduor et al. 2010, Cole and Litton 2014). The introduction of non-native ungulates has led to extensive changes in vegetation cover and wide spread loss of native plant species globally (Courchamp et al. 2003). Moreover, non-native ungulate invasions are frequently associated with subsequent

invasion by non-native plants across a broad range of ecosystems (Parker et al. 2006), perhaps in response to increased soil nutrient availability in the presence of non-native ungulates (Spear and Chown 2009). Non-native invasive plants, in turn, can also alter ecosystem processes and completely replace native species (Vitousek et al. 1987b).

The direct and indirect impacts that non-native ungulates have on ecosystems is evident on islands globally, including throughout the Hawaiian archipelago (Banko et al. 2014). The recognized negative impact of non-native ungulates has resulted in a management strategy that typically includes ungulate removal as a critical early step in ecological restoration (Banko et al. 2014). However, the removal of non-native ungulates alone is typically not enough (Loope and Medeiros 1994, Cabin et al. 2000, Bullock et al. 2002, Donlan et al. 2002), and additional management actions may be necessary (e.g., non-native plant control, reintroduction of key native species, alteration of resource availability) (Weller et al. 2011).

Hawaiian Wet and Dry Ecosystems

The Hawaiian Islands are the most isolated archipelago on Earth. Hawaii is considered a model system for ecological research because of its well-defined biotic and abiotic gradients, it's relatively simplistic ecosystems in terms of species diversity, and abundant examples of adaptive radiation (Vitousek 2004). Additionally, because of its isolation Hawaii is especially vulnerable to human caused disturbances and subsequent invasion by non-native plants. It is also home to many endemic and endangered species, making restoration of invaded ecosystems critical for biological conservation.

Remnant native Hawaiian forests occur increasingly in isolated fragments and degraded areas, where they face constant threats from nonnative, invasive ungulates, rodents and plants, as well as a human-modified wildfire regime (Cuddihy and Stone 1990, Smith and Tunison 1992, Price and Morgan 2007, Trauernicht et al. 2015). Moreover, native species continue to decline in many areas due to a lack of natural regeneration, at least partially as a result of competition with non-native plants (Cabin et al. 2000, Cabin et al. 2002a, Cabin et al. 2002b, Litton et al. 2006, Zimmerman et al. 2008, Cordell et al. 2009). For example, Hawaiian tropical dry forests have been reduced and fragmented as a result of land use change, wildfire, and invasion by non-native species (Wagner et al. 1999), with

<10% remaining intact (Bruegmann 1996) yet the highest proportion of endangered taxa among all Hawaiian plant communities (Sakai et al. 2002). In particular, remnant dry forests are largely found on the Island of Hawaii and are typically heavily invaded by *Cenchrus setaceus* (Forssk.) Morrone (fountain grass; formerly *Pennisetum setaceus*), a C_4 perennial bunchgrass from North Africa (Wagner et al. 1999). *C. setaceus* limits the recruitment and growth of native species via competition for light and water (Cabin et al. 2000, Cordell and Sandquist 2008, Litton et al. 2008, Thaxton et al. 2010), and facilitates wildfires that result in type conversions from highly diverse native forests to monotypic, non-native grasslands.

Hawaii's native wet ecosystems also occur increasingly in fragments (Price and Morgan 2007), which are continuously threatened by land use change and feral ungulates such as pigs (Wagner et al. 1999), and invasive plants such as *Psidium cattleianum* Sabine, which collectively limit regeneration of native species (Zimmerman et al. 2008, Cordell et al. 2009). Feral pig rooting and digging, in particular, provide an opportunity for a variety of non-native invasive plants to establish, including *P. cattleianum* (Wagner et al. 1999). The establishment and spread of *P. cattleianum* has had major impacts on Hawaii's wet forests, specifically on the two dominant wet forest canopy species *Acacia koa* A. Gary and *Metrosideros polymorpha* Gaudich (Wagner et al. 1999). Once established in dense stands, *P. cattleianum* limits regeneration by native species, presumably due to low light levels under its canopy (Wagner et al. 1999).

Study Overview

The widespread establishment and spread of invasive species in Hawaii's native wet and dry ecosystems, especially for the most problematic species such as *C. setaceus* and *P. cattleianum*, stresses the need to develop restoration methods to restore native ecosystems by promoting native over non-native species. To this end, I conducted a greenhouse experiment with the objectives to: (*i*) determine the growth response of native and nonnative, invasive species to varying soil nutrient levels, (*ii*) determine if native and nonnative, invasive species display differences in RUE plasticity in response to varying soil nutrients, and (*iii*) determine if soil nutrients limit photosynthesis and the photosynthetic response of native and nonnative, invasive species to varying soil nutrient levels. These

three objectives were examined to help determine if soil nutrient manipulation may be successful as a restoration technique for promoting native species in invaded ecosystems.

The greenhouse experiment was conducted at the Institute of Pacific Islands Forestry, in Hilo on the Island of Hawai'i. Five nutrient treatments were applied to native and non-native invasive plants common to Hawaiian tropical dry and wet ecosystems. The five treatments applied included two nutrient reduction treatments, a control (i.e., background nutrient levels), and two nutrient addition treatments. Plant density in experimental pots was kept constant at 2, and species were grown with a conspecific or with the most common invader from that ecosystem type (*C. setaceus* in dry ecosystems, and *P. cattleianum* in wet ecosystems). Biomass, survival, reproductive output, plant physiological traits (whole plant carbon gain, G_s, C_i, V_{cmax}, and J_{max}) and resource use efficiency were quantified across the five nutrient treatments to address species responses to varying soil nutrient availabilities and to determine if soil nutrient manipulation may be a useful restoration technique for woody species in tropical ecosystems.

Chapter 2

Linking growth and physiological responses of native and nonnative, invasive plants to soil nutrient availability

Abstract

Native ecosystems worldwide face constant pressure from nonnative, invasive plants that are often competitively superior. In particular, evidence exists that nonnative plants typically outcompete natives in a variety of ecosystems under conditions of high resource availability. Therefore, one potential restoration technique favoring native species over nonnatives could be to decrease soil nutrient availability via carbon amendments when nutrient levels are elevated (e.g., following a disturbance). This is an appealing concept in Hawai'i where native species often have conservative growth strategies, but this idea has received very little attention to date, particularly in tropical ecosystems. I evaluated survival, growth, reproductive output, resource use efficiency (RUE), and ecophysiology of native and nonnative, invasive species from Hawaiian wet (*Acacia koa, Metrosideros polymorpha,* and *Psidium cattleianum* (invasive)) and dry (*Dodonaea viscosa, Metrosideros polymorpha, Sophora chrysophylla,* and *Cenchrus setaceus* (invasive)) ecosystems in a greenhouse experiment. The density of plants was held constant (two plants/pot), and native species were grown for 6-12 months with a conspecific and with the ecosystem-specific invasive species in each of five soil nutrient treatments (control; high and low nutrient addition via fertilizer; and high and low nutrient reduction via carbon amendments). Results show that biomass, whole plant carbon gain, and foliar nutrient content of all species across both ecosystem types increased with increasing soil nutrient availability. When individual growth and plant carbon gain responses were examined, all native species had a non-significant response to soil nutrient level, except *D. viscosa*. *D. viscosa* and both nonnatives, *C. setaceus* and *P. cattleianum,* responded similarly with total biomass and whole plant carbon gain increasing with increasing soil nutrient availability. *M. polymorpha* experienced very high mortality in both nutrient addition treatments (mean of 86% mortality). The nonnative grass *C. setaceus* displayed a sharp decrease in reproductive output with decreasing soil nutrient availability, with a 65% flowering rate in nutrient addition treatments and a 3% flowering rate in nutrient

reduction treatments. Measurements of photosynthetic capacity (V_{cmax} and J_{max}) were constant for all species across varying soil nutrient levels. RUE of native species remained constant, while that of invasive species decreased with decreasing soil nutrient availability. Collectively, these results suggest that reducing soil nutrient availability is a promising technique for restoring native Hawaiian ecosystems where nutrient availability is high and invasive species are a concern.

Introduction

The invasion of non-native species is one of the most serious threats to biodiversity and ecosystem function globally (Millennium Ecosystem Assessment 2005). Invasive species can alter biological diversity, ecosystem processes, and the physical environment in ways that promote further invasion and reduce ecosystem services (Vitousek et al. 1996). Invasive species are particularly problematic on small and remote oceanic islands, such as Hawaii, where a large majority of native species are endemic (Paulay 1994). Native Hawaiian ecosystems occur in increasingly isolated fragments that are heavily impacted by invasive species (Cabin et al. 2000, Cabin et al. 2002a, Cabin et al. 2002b, Litton et al. 2006). Changes in nutrient availability (e.g., following a disturbance) can also promote invasion by nonnative plants (D'Antonio and Vitousek 1992, Ehrenfeld 2003, Foley et al. 2005). Invasive species are typically thought to invade areas of high resource availability, owing their success in these environments to traits of rapid resource uptake and utilization. But the success of an invasive species is also context dependent and the mechanisms associated with their success can vary between resource-rich and resource-poor environments (Daehler 2003). Understanding how soil resource availability impacts competition between native and invasive species is critical for successfully managing invasive species.

There is not a single trait or suite of traits that can universally explain how a plant species becomes invasive, largely because traits of successful invaders often depend on characteristics of the invaded habitat (Pysek et al. 1995, Alpert et al. 2000, Daehler 2003, Pyšek and Richardson 2010). However, there are numerous traits associated with invasion success that collectively highlight a resource-exploitative strategy, including high relative growth rate (Burns 2004, Garcia-Serrano et al. 2005, Burns 2006, Gurevitch et al. 2008), low leaf mass per unit area (Pammenter et al. 1986, Durand and Goldstein 2001, Grotkopp

and Rejmánek 2007), and high photosynthetic rate (Baruch and Goldstein 1999, McDowell 2002, Funk and Vitousek 2007). These traits complement the observation that invasive species commonly invade areas of high resource availability (Burke and Grime 1996, Daehler 2003), which often occur following a disturbance. However, invasive species have also been observed invading and outcompeting native species in environments of low resource availability (Pavlik 1983, Pammenter et al. 1986, Funk and Vitousek 2007, Matzek 2011, Heberling and Fridley 2016). In low resource environments invasive species have been observed to have advantageous functional traits independent of resource availability (Heberling and Fridley 2016). Invasive species present in nutrient-poor and nutrient-rich soils, for example, often utilize different mechanisms for nutrient uptake, and these differences may explain their success under widely varying soil nutrient availabilities. Prior research also shows that at least some invasive species present in low nutrient environments employ resource conservation strategies more typical of slower-growing native species, such as high nutrient-use efficiency, high resistance to low nutrient levels, and high trait plasticity (Funk and Vitousek 2007, Schumacher et al. 2009, González et al. 2010, Matzek 2011).

Functional traits associated with resource conservation are typically displayed in slower growing native species adapted to low resource environments. Many of these species have evolved mechanisms to tolerate stress and aid in the uptake of limiting resources in low resource environments, and these adaptations appear to give native species an advantage over invasive species under these conditions (Alpert et al. 2000, Daehler 2003). These resource conservation traits generally slow plant growth rates but increase resource use efficiency (RUE; carbon assimilation per unit of resource). Resource conservation traits typically include long leaf lifespans, high leaf mass per unit area (LMA), low rates of photosynthesis, high levels of defense compounds, low tissue nutrient content, and/or thicker leaves (Vitousek 1982, Coley et al. 1985).

In systems where native plants exhibit resource conservation strategies and nonnative, invasive species exhibit resource exploitation strategies, decreasing soil nutrient availability may help inhibit invasive species and facilitate native species by altering competitive dynamics (Blumenthal et al. 2003, Burke et al. 2013). One method for decreasing soil nutrients is to promote the uptake of available inorganic nitrogen by soil

microbes through the application of a metabolic substrate that is high in carbon and low in nutrients, such as sucrose, cellulose, or sawdust (Alpert 2010). Because soil microbes use carbon and nitrogen to maintain a specific ratio of carbon to nitrogen (C:N), adding carbon to the substrate will increase the microbes demand for nitrogen resulting in the immobilization of inorganic nitrogen in microbial biomass, and a subsequent reduction in the availability of soil nutrients to plants. While multiple studies have shown that carbon amendments can be effective in stimulating nitrogen immobilization and reducing soil nitrogen availability (Gallardo and Schlesinger 1995, Schaeffer et al. 2003, Alpert 2010, Perry et al. 2010, Burke et al. 2013), the effects of reduced soil nutrient availability on native vs. invasive species has been mixed. The most successful studies have shown that carbon amendments increase native biomass while decreasing invasive biomass (Allen and Zink 1998, Blumenthal et al. 2003, Perry et al. 2004, Prober et al. 2005b, Eschen et al. 2007). But other studies have shown that carbon amendments can reduce native species growth as much or more than invasive species (Morghan and Seastedt 1999, Monaco et al. 2003, Suding et al. 2004, Gendron and Wilson 2007). Differences in responses to altered soil nutrient availability can often be related to the physiology of the study plants and overall site resource conditions, but this has rarely been examined (Steers et al. 2011).

The majority of research that has looked at soil nutrient manipulation as a restoration tool has not done so in the context of RUE, and in so doing lacks a mechanistic context. In addition, the effect of carbon amendments on native vs. invasive species competition in tropical systems and, in general, with woody species has received very little attention (Alpert 2010), making the potential viability of this restoration technique unclear in tropical systems and/or with woody species. To address these information gaps, I examined the effects of varying soil nutrient availability on woody species common in tropical Hawaiian wet and dry ecosystems in a greenhouse study, with the overarching goal to determine if soil nutrient manipulation may be a successful restoration tool for invaded tropical ecosystems dominated by woody species. Theoretically for nutrient manipulation to promote native species over nonnative, invasive species, the resource use strategies of native vs. nonnative invasive species must differ. For example, this approach will be the most successful where native species are generally resource conservative, and nonnative, invasive species are generally resource exploitative (Burke and Grime 1996, Daehler 2003).

Therefore, this study had three major objectives: (*i*) determine the growth response of representative native (presumed to be resource conservative) and nonnative, invasive species (presumed to be resource exploitative) to varying soil nutrient levels, (*ii*) determine if native and nonnative, invasive species display differences in RUE plasticity in response to varying soil nutrients, and (*iii*) determine if soil nutrients limit photosynthesis and the photosynthetic response of native and nonnative, invasive species to varying soil nutrient levels.

Increased nutrient availability often facilitates the establishment and growth of fast growing invasive species adapted to high resource availability (i.e., resource exploitative) (Davis et al. 2000), while native species adapted to low resource availability are often less able to take advantage of increased resource availability (Vitousek et al. 1987b, Hobbs and Huenneke 1996). In addition, under varying resource conditions native species have shown adaptive fitness responses compared to invasive species, resulting in smaller declines of fitness related traits in response to environmental conditions such as nutrient limitation (i.e., resource conservative) (Davidson et al. 2011). Therefore my first hypothesis was that across all native and nonnative species from tropical dry and wet ecosystems, reduced nutrient availability via carbon amendments would decrease plant growth, while increased nutrient availability via fertilizer would increase plant growth. Across ecosystem types it was also hypothesized that native species would show a more neutral response (i.e., smaller changes in total biomass) to changes in nutrient availability, whereas invasive species would show a stronger response (i.e., larger changes in total biomass) to changes in nutrient availability, in line with resource conservative and exploitative strategies, respectively. Additionally, it was hypothesized that there would be no relationship between intraspecific competition and soil nutrient availability (i.e., native and nonnative species grown with a congener), but that when species were in interspecific competition (i.e., native and nonnative species in direct competition) increasing soil nutrient availability would result in increased differences (i.e., delta values) in biomass as a result of differences in resource use strategy (i.e., resource conservative vs. exploitative).

Invasive species have been shown to have higher photosynthetic capacity than native species under various resource availabilities (McDowell 2002, Heberling and Fridley 2016). Additionally, studies have shown that with decreased soil nutrient availability, J_{max}

and V_{cmax} decrease (Zhang and Dang 2006). Therefore, my second hypothesis was that across all tropical dry and wet ecosystem native and nonnative plants, reduced nutrient availability would decrease photosynthesis but invasive species would show a stronger response compared to native species (i.e. larger changes in photosynthesis in invasive species in response to soil nutrient availability). Additionally, across ecosystem types I hypothesized that V_{cmax} and J_{max} would be limited by soil nutrient availability and decrease with decreasing soil nutrients. Further, invasive species were hypothesized to have higher V_{cmax} and J_{max} than native species across all soil nutrient availabilities. My final hypothesis was that across ecosystem types, the RUE of native species would remain constant with soil nutrient availability, whereas the RUE of invasive species would decrease with increasing nutrient availability. Recent studies have shown native species to be unresponsive in RUE to changes in resource availability (Davidson et al. 2011, Heberling and Fridley 2016). Conversely, RUE in invasive species has been shown to be more plastic in response to changes in resource availability (Funk 2008, Davidson et al. 2011, Heberling and Fridley 2016), for example by employing resource conservation strategies when present in low resource environments (Funk and Vitousek 2007).

Methods

This study was conducted at the Institute of Pacific Islands Forestry (IPIF) greenhouse facility in Hilo, HI (19°41'55.6"N 155°05'43.5"W), located on the windward side of the Island of Hawaii at 109 m asl. Two parallel experiments were run from June 2014 to June 2015 using common native and nonnative species, primarily woody species, from both wet and dry ecosystems in Hawaii. *Dodonaea viscosa* Jacq., *Metrosideros polymorpha* Gaud., and *Sophora chrysophylla* (Salisb.) Seem. were utilized as the common native species for the dry ecosystem, and *Acacia koa* A. Gray and *M. polymorpha* as the common native species for the wet ecosystem. *Cenchrus setaceus* (Forssk.) Chiov. and *Psidium cattleianum* Sabine were utilized as the common nonnative, invasive species for the dry and wet ecosystems, respectively. Species were selected based on the availability of seedlings, capacity for propagation, and dominance in each ecosystem type. Native species used are dominant woody canopy species of the ecosystems in which they are found. The nonnative invasive species utilized (a small tree and a grass) typically invade understories

of native Hawaiian ecosystems, but over time can become canopy dominant through alterations in competition and regeneration. All seedlings were sourced from local nurseries expect *P. cattleianum* and *C. setaceus* (Appendix A). *P. cattleianum* seedlings were collected from local stands surrounding IPIF. Live clumps of *C. setaceus* were collected from Saddle Road between Hilo and Kona, and separated into small individuals. Once collected, both species were planted in standard potting soil approximately five weeks prior to the start of the study to promote establishment in the greenhouse.

Two-gallon pots were planted at a constant density of two plants per pot, and each species was planted with a conspecific and the common invasive species from that ecosystem type. Each species combination was replicated eight times across the five nutrient treatments for a total of 280 experimental planting pots for the dry ecosystem and 200 for the wet ecosystem. In June 2014, all woody seedlings were directly transplanted into pots representing one of five soil nutrient availability treatments: nutrient reduction high, nutrient reduction low, control, nutrient addition low, and nutrient addition high. *C. setaceus* clumps were separated into individual plants of approximately the same size prior to planting (mean individual initial weight of ~4.4 g). Soil nutrient availability treatments (Appendix B) were mixed into pots containing ~3.14kg of a 50:50 soil:cinder mixture containing Pepeekeo topsoil of the Hilo Soil Series from the Hamakua Coast. These are deep, well drained soils that formed from weathered volcanic ash, and are classified as medial over hydrous, ferrihydritic, isohyperthermic Acrudoxic Hydrudands (Soil Staff Survey 2016).

Nutrient reductions were implemented through the application of carbon amendments. Both sucrose and sawdust were used to reduce nutrient availability rapidly and throughout the experiment. Sucrose was obtained in the form of table sugar from local grocery stores and sawdust from a local mill as a mixture of *Eucalyptus robusta* and *A. koa*. Target C:N ratios were determined to represent high (C:N ~35) and low (C:N ~20) levels of N immobilizations from an initial soil C:N of 13.5, and these target C:N values were used to determine the amount of sucrose and sawdust needed for the target C:N (Appendix B). Nutrient addition treatments were implemented using Apex 16-6-12 NPK slow-release fertilizer, following the manufacturer recommendation of 15g fertilizer/two-gallon pot (low nutrient addition treatment), which was then doubled, to 30g/pot for the high

nutrient addition treatment. All soil nutrient availability treatments were mixed into the soil prior to planting to create a homogenous mixture throughout each pot. In addition to the four soil nutrient treatments, a control treatment was used with no manipulation of soil nutrients (Appendix B).

Pots were arranged randomly in the greenhouse into four blocks. Every three months, pots were rotated in a counter clockwise fashion to eliminate any possible shading effect. Plants were watered to field capacity regularly so that water was not a limiting resource, and were monitored for disease and insect problems weekly and treated as necessary. Initial plant measurements (height, basal diameter, and canopy cover for all species except *C. setaceus* individuals, which were weighed due to the propagation method) were conducted at the time of planting to see if differences existed at the start of the study despite random assignment to treatments. The dry ecosystem study was ended after 6 months (i.e., plants too large for the pots at that point), while the wet ecosystem study ran for one year.

Growth measurements

All plants were destructively harvested to obtain final belowground, aboveground and total biomass. Roots were rinsed thoroughly to remove soil. All plant material was dried to a constant mass in a forced-air oven at 60° C and weighed. Plant mortality was quantified weekly throughout the experiment. Additionally, reproductive output (i.e., flowers and/or fruits) was recorded bi-monthly. The number of flowers on each individual was tallied, and reproductive tissue was harvested, dried, and weighed.

Photosynthetic capacity

Leaf-level gas exchange (maximum photosynthetic rate (A_{max}), stomatal conductance (g_s), and intercellular CO_2 levels (C_i)) was measured on one leaf from the most recently expanded cohort ~6 months after experiment initiation in December 2014 and prior to harvest of dry ecosystem pots. Measurements were made with a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE), on three randomly chosen pots in each treatment for each species combination (i.e., n=3 for gas exchange measurements). The following conditions were maintained during measurements: light fully saturated (1,000

μmol m^{-2} s^{-1}), CO_2 concentration of 400 ppm, relative humidity between 55 and 65%, and temperature reflective of ambient greenhouse conditions. To scale up individual leaf A_{max} to whole plant carbon gain, the six most recent fully expanded leaves were collected, analyzed on a leaf area meter, dried at 60°C to a constant mass, and weighed. The weight to area ratio for these six leaves was then used to scale photosynthesis to whole plant carbon gain based on the total weight of individual plant foliage determined from the destructive biomass harvest.

A/C_i curves were completed on both individuals from one randomly chosen pot (n=1) for each species combination in the nutrient addition high, nutrient reduction high, and control treatments to obtain maximum carboxylation capacity (V_{cmax}) and maximum rate of chloroplast electron transport (J_{max}). Measurements of A were taken under CO_2 concentrations of 420, 300, 200, 100, 50, 420, 420, 600, 800, 1200, and 2000 ppm. The values of A at each CO_2 concentration were then analyzed with Photosynthesis Assistant software (Dundee Scientific, UK) to obtain associated V_{cmax} and J_{max} values.

Resource Use Efficiency

Foliar samples collected for leaf area measurements were also used for nutrient analyses to determine resource use efficiency (RUE). Additional foliage was collected for nutrient analyses in the same manner as described above when the dry mass of the first six leaves was < 0.25 g (the minimum sample size for nutrient analyses). Leaf samples were dried at 60°C to a constant mass, weighed, ground into a fine powder with a ball mill, and analyzed at the University of Hawaii at Hilo Analytical Lab (UHHAL) for %P analysis, and Cornell Stable Isotope Lab (COIL) for %C and %N analyses. The whole plant carbon gain and foliar %N and %P was utilized to determine photosynthetic nitrogen use efficiency (PNUE) and photosynthetic phosphorous use efficiency (PPUE) for each individual as:

$$PNUE = Whole\ Plant\ Carbon\ Gain \div \%N$$

$$PPUE = Whole\ Plant\ Carbon\ Gain \div \%P$$

Statistical Analysis

Linear regression models were used to analyze biomass, photosynthetic parameters, and RUE response variables across the soil nutrient treatments for all plants combined and

for each species separately. For all regression models, the mean initial C:N for a given nutrient treatment was used as a continuous independent variable. All tests were performed on the mean of each response variable for each species in a given nutrient treatment. The response of competitive dynamics to soil nutrient availability was analyzed with the delta value of total biomass for species grown in both intra- and interspecific competition. At the start of the experiment plants were identified as either plant A or plant B, such that:

$$Delta\ (Total\ Biomass) = Plant\ B - Plant\ A$$

Deltas were then analyzed with a linear regression to determine the effect of soil nutrient availability on the competitive dynamics of each species.

Data that did not meet model assumptions of homogeneity of variance were log transformed. Initial plant conditions (height, basal diameter, and canopy cover) were analyzed with a one-way analysis of variance (ANOVA) to check for homogeneity across treatments at the start of the study. Despite being randomly assigned to treatments, initial plant size differed with soil nutrient treatment at the start of this study for all species except *C. setaceus* (Appendix C). As a result, initial plant conditions (i.e. initial height, basal diameter, and canopy cover) were included in the regression analysis as predictors for analyses of total biomass to account for the initial differences in plant size across the soil nutrient availability treatments (i.e., C:N). Pots with mortality were not used for data analysis outside of survival.

Reproductive output and mortality were analyzed using a binary logistic regression. Minitab 17.2.1 (Minitab Inc., State College, PA, USA) was used for all statistical analyses, and significance was determined at a=0.05.

Results

Growth responses

Across both the wet and dry ecosystems and for all species combined, increasing soil nutrient availability increased plant growth (F = 123.39, P < 0.01, r^2= 0.22, n = 449). As soil nutrient availability increased by one unit of C:N, plant growth increased by 10% (Appendix D). For all species except *C. setaceus* and *P. cattleianum*, there was no relationship between intraspecific competition and soil nutrient availability. That is, the

delta values for total biomass did not vary with soil nutrient availability ($P > 0.05$). For both *C. setaceus* ($F = 25.40$, $P < 0.01$, $r^2 = 0.40$, $n = 40$) and *P. cattleianum* ($F = 13.35$, $P < 0.01$, $r^2 = 0.28$, $n = 35$), the delta values of biomass increased with soil nutrient availability (Fig. 1a & 1b). A relationship was found between interspecific competition and soil nutrient availability, in general as soil nutrient availability increased the delta for total biomass between native and invasive species increased (Fig. 2a & 2b). A significant difference was present in the deltas for all interspecific competition species combinations ($P < 0.05$), except for the *P. cattleianum* with *A. koa* combinations ($F = 2.39$, $P = 0.08$, $r^2=0.25$, $n = 33$).

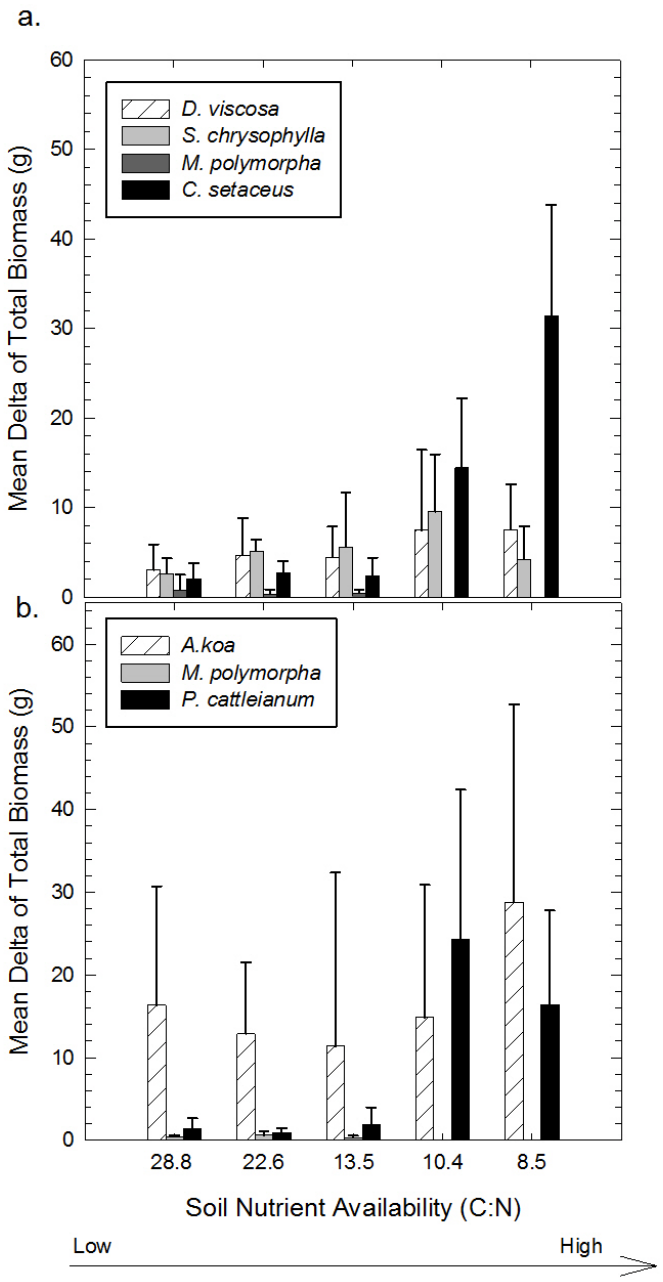

Figure 1. Mean delta of total biomass for dry (a) and wet (b) ecosystem species in intraspecific competition. Deltas represent the difference in total biomass of the two congeneric species in a single pot.

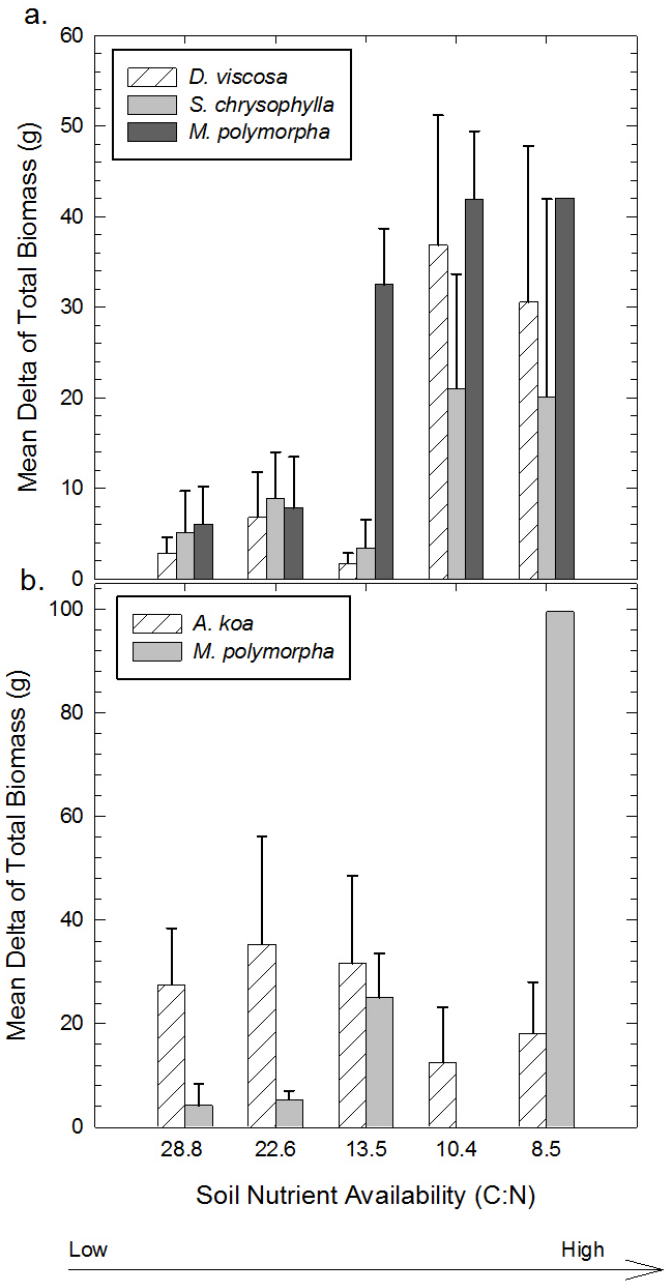

Figure 2. Mean delta of total biomass for dry (a) and wet (b) ecosystem species in interspecific competition. Deltas represent the difference in total biomass of the native and nonnative species in a single pot.

Because there was a difference in the response of intraspecific vs. interspecific competition to variation in soil nutrient availability, individual species biomass results are presented separately for intraspecific vs. interspecific competition pots. Native species from both the wet and dry ecosystems showed a more neutral growth response to soil nutrient availability than the nonnative, invasive species, except for the natives *D. viscosa* and *M. polymorpha* (Fig. 3-4). *M. polymorpha* was utilized in both the wet and dry ecosystem studies because of it's widespread occurrence and dominance across a range of ecosystem types in the Hawaiian Islands, and this species underwent significant mortality as soil nutrient availability increased ($P < 0.01$, *Chi-square* = 98.28, $r^2 = 0.45$), with up to 100% mortality in nutrient addition treatments (Fig. 5). In the nutrient reduction and control treatments, mortality of *M. polymorpha* was much lower and ranged from 0 to 38% across both ecosystem types. Mortality of all other species was low and did not vary with soil nutrient availability treatments, ranging from 0 to 33% across species, treatments and ecosystem types. *D. viscosa's* biomass increased approximately 8% as nutrients increased (i.e., every one unit decrease in C:N)($F = 61.43$, $P < 0.01$, $r^2 = 0.66$, $n = 34$) in intraspecific competition, compared to an 11% increase as nutrients increased in interspecific competition ($F = 49.63$, $P < 0.01$, $r^2 = 0.60$, $n = 34$). For both *A. koa* and *S. chrysophylla*, changes in total biomass in response to soil nutrient availability were not significant, and this was the case for both intraspecific and interspecific competition (Fig. 3-4).

Nonnative, invasive species showed stronger responses to soil nutrient availability compared to native species. The total biomass of *P. cattleianum* increased by ~12% as soil nutrients increased (i.e. for every one unit decrease in C:N) ($F = 30.93$, $P < 0.01$, $r^2 = 0.48$, $n = 35$), in intraspecific competition, compared to a ~15% increase in biomass as soil nutrients increased in interspecific competition ($F = 73.88$, $P < 0.01$, $r^2 = 0.59$, $n = 54$) (Fig. 3b & 4b). *C. setaceus* total biomass also increased by ~12% in response to increased soil nutrient availability (i.e. a one unit decreased in C:N) in intraspecific competition ($F = 35.34$, $P < 0.01$, $r^2 = 0.52$, $n = 35$), and ~8% in interspecific competition ($F = 32.36$, $P < 0.01$, $r^2 = 0.28$, $n = 87$) (Fig. 3a & 4a). Further, *C. setaceus* was the only species to produce reproductive output, where reproductive output increased with soil nutrient availability ($P < 0.01$, *Chi-square* = 73.87, $r^2 = 0.37$), to as high as 80% of individuals with increased soil nutrient availability (Fig. 6).

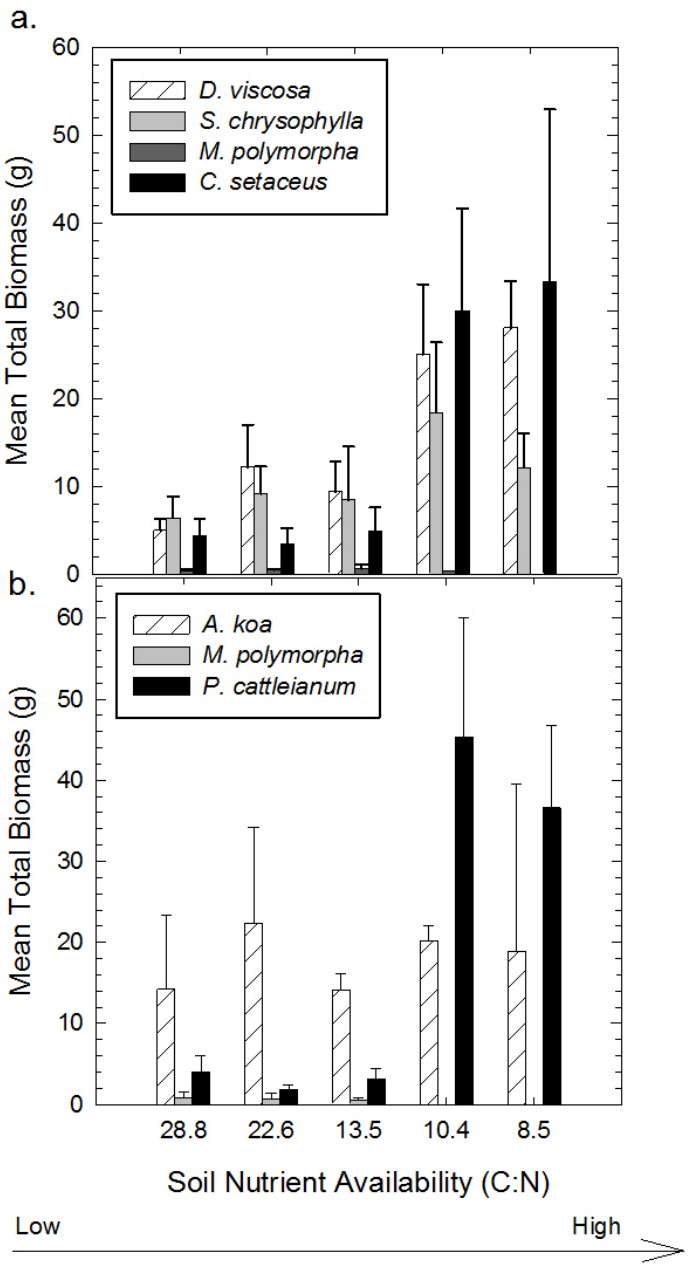

Figure 3. Mean total biomass for each species in intraspecific competition. Biomass responses to changes in soil nutrient availability were significant for *D. viscosa, C. setaceus*, and *P. cattleianum*.

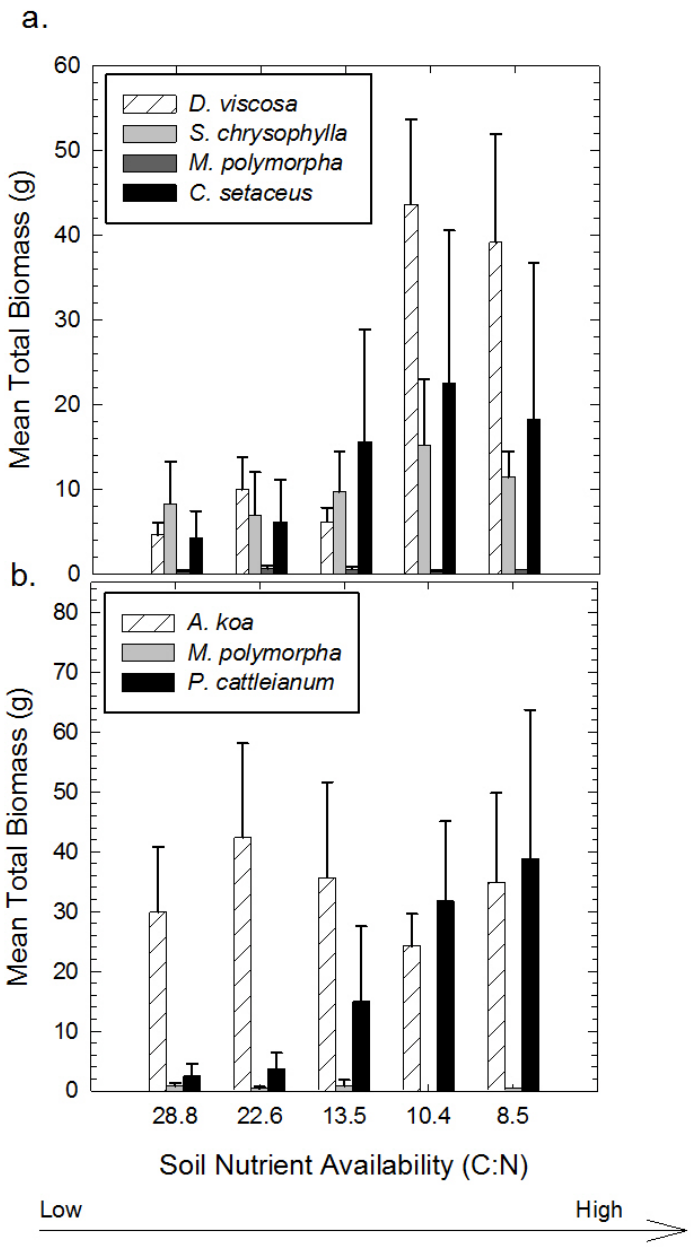

Figure 4. Mean total biomass for each species in interspecific competition. Biomass responses to changes in soil nutrient availability were significant for *D. viscosa, C. setaceus*, and *P. cattleianum*.

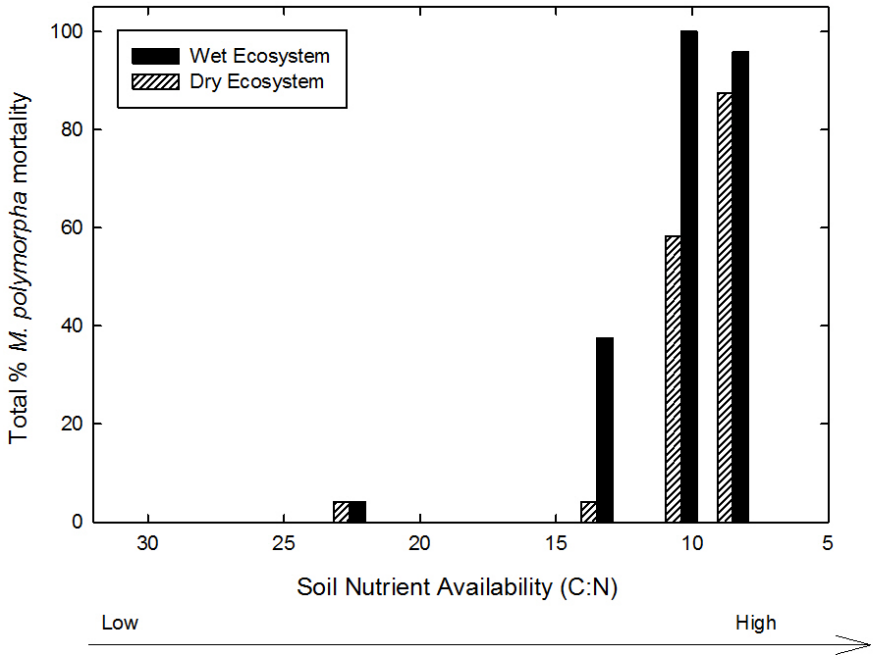

Figure 5. Total percent mortality of *M. polymorpha* across all nutrient availabilities for both the wet and dry ecosystems. No mortality occurred in the high nutrient reductions treatments (C:N = 28.8).

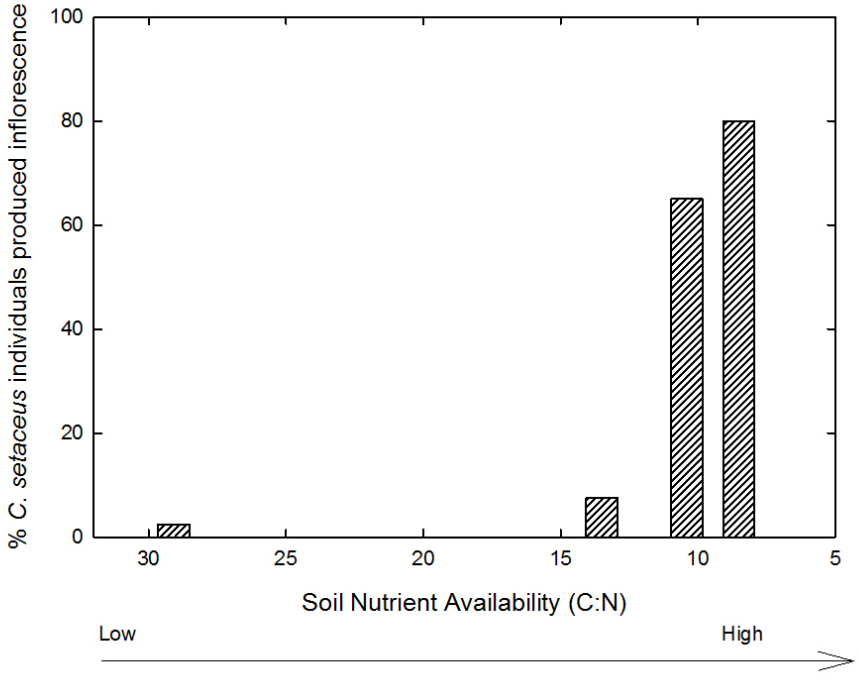

Figure 6. Total percent of *C. setaceus* individuals that produced inflorescences.

Photosynthetic capacity

Foliar nitrogen (F =76.04, P < 0.01, r^2 = 0.21, n = 235) and phosphorus (F =18.94, P < 0.01, r^2 = 0.08, n = 230) content increased with increasing soil nutrient availability across all plants in both ecosystem types (Fig. 7). Whole plant carbon gain also increased with increasing soil nutrient availability (F = 23.14, P < 0.01, r^2 = 0.09, n = 235) across all plants in both ecosystem types with whole plant carbon gain increasing by 7% per unit increase in soil nutrient availability (Appendix D). Stomatal conductance (G_s) and intercellular CO_2 (C_i) showed no significant response to changes in soil nutrient availability across all species from both ecosystem types. Whole plant carbon gain, G_s, and C_i did not vary with soil nutrient availability for any individual native species except *D. viscosa* (Fig. 8). *D. viscosa* whole plant carbon gain increased with increasing soil nutrient availability by 8% per unit C:N (F = 15.35, P < 0.01, r^2 = 0.31, n = 36) (Figure 8a). Both G_s and C_i of *D. viscosa* increased with decreasing soil nutrient availability, by 6% (F = 14.53, P < 0.01, r^2 = 0.30, n = 36) and 3.5% (F = 22.37, P < 0.01, r^2 =0.40, n = 36), respectively, per unit change in soil nutrients.

The photosynthetic response of nonnative, invasive species to soil nutrient availability was stronger than that for native species. As soil nutrient availability increased (i.e. per unit decrease in C:N), whole plant carbon gain in *P. cattleianum* and *C. setaceus* increased by 10% (F = 11.40, P < 0.01, r^2 = 0.23, n = 40) and 8% (F = 12.10, P < 0.01, r^2 = 0.17, n = 62), respectively (Fig. 8). G_s and C_i for *C. setaceus* did not vary with soil nutrients. However both variables increased with decreasing soil nutrient availability for *P. cattleianum*. Across all species and both ecosystem types, V_{cmax} (F = 0.41, P = 0.53, r^2 = 0.84, n = 50) and J_{max} (F = 0.33, P = 0.57, r^2 = 0.69, n = 50) did not vary with soil nutrient availability. Differences in V_{cmax} and J_{max} observed were independent of soil nutrient availability. Of all species examined, the native *A. koa* had the highest mean V_{cmax} and J_{max} of all species and the native *D. viscosa* had the lowest (Table 1).

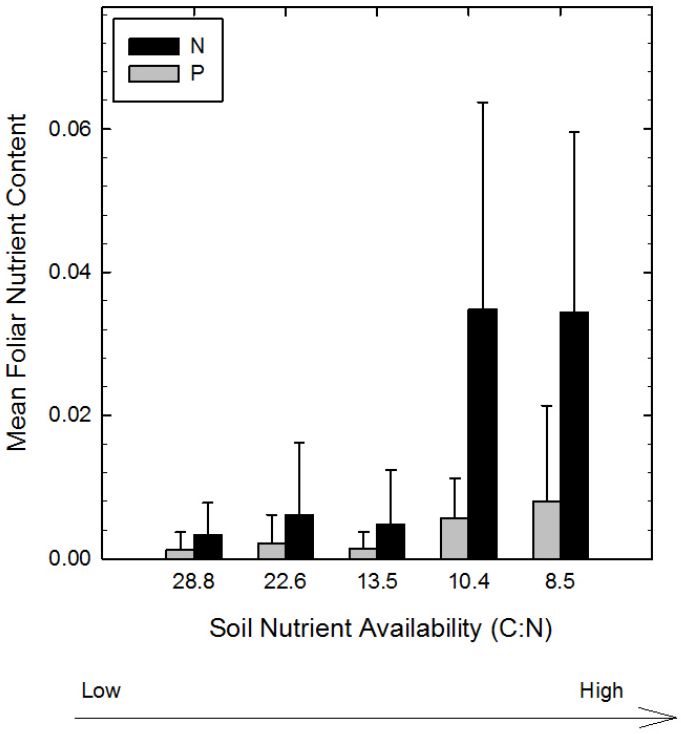

Figure 7. Foliar nitrogen and phosphorus content for all species across soil nutrient availability. Both nitrogen and phosphorus content had a significant relationship with soil nutrient availability, and foliar content increased with increasing soil nutrients.

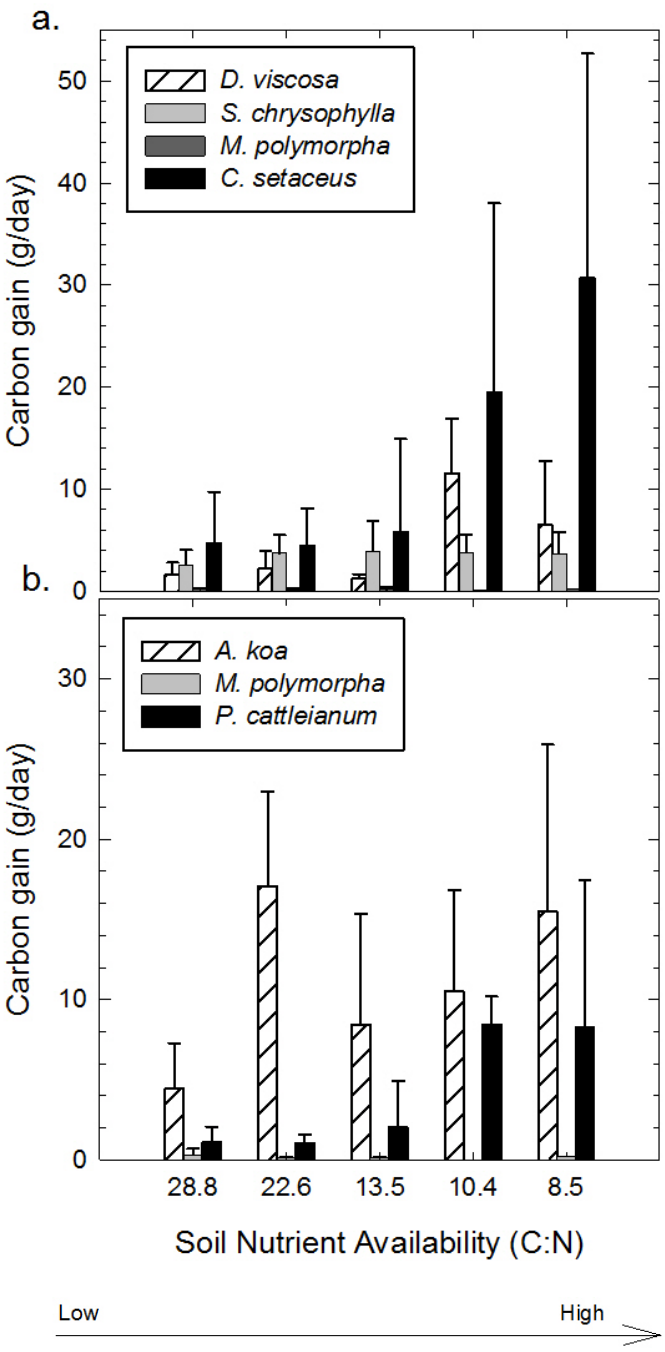

Figure 8. Mean carbon gain for each species in the dry (a) and wet (b) ecosystem. Carbon gain responses to changes in soil nutrient availability were significant for *D. viscosa, C. setaceus*, and *P. cattleianum*.

Table 1. Table 1. Mean V_{cmax} and J_{max} for all species. No species significantly responded to soil nutrient availability but differences were present among species. *Indicate species with significantly different V_{cmax} and J_{max}.

Species	**Mean V_{cmax}, (+ 1 S.D.)**	**Mean J_{max}, (+ 1 S.D.)**
A. koa	46.68 (18.22)*	250.30 (69.00)*
C. setaceus	27.40 (16.74)	106.3 (64.00)
D. viscosa	15.85 (5.68)	66.70 (20.33)
M. polymorpha	19.93 (7.85)	79.25 (30.83)
P. cattleianum	25.22 (8.25)	104.60 (37.20)
S. chrysophylla	24.14 (13.67)	100.5 (64.10)

Resource Use Efficiency

Photosynthetic nitrogen use efficiency (PNUE) and phosphorus use efficiency (PPUE) remained constant across soil nutrient availabilities for all native species, with the exception of PPUE in *D. viscosa* which decreased by 10% for every unit decrease in soil nutrient availability ($F = 20.32$, $P < 0.01$, $r^2 = 0.37$, $n = 36$) (Fig 9–10). For the nonnative, invasive species tested, PNUE and PPUE generally decreased with decreasing soil nutrient availability. As soil nutrients decreased (i.e., per unit increase in C:N) PPUE of *C. setaceus* decreased by approximately 10% ($F = 14.90$, $P < 0.01$, $r^2 = 0.21$, $n = 59$)(Fig. 10a). PNUE of *C. setaceus* did not vary with soil nutrients (Fig. 9a). *P. cattleianum* PPUE decreased by ~14% ($F = 16.63$, $P < 0.01$, $r^2 = 0.32$, $n = 38$) and PNUE decreased by 10% ($F = 13.50$, $P < 0.01$, $r^2 = 0.27$, $n = 39$) as soil nutrients decreases (i.e., every one unit change in soil nutrients) (Fig. 9b & 10b).

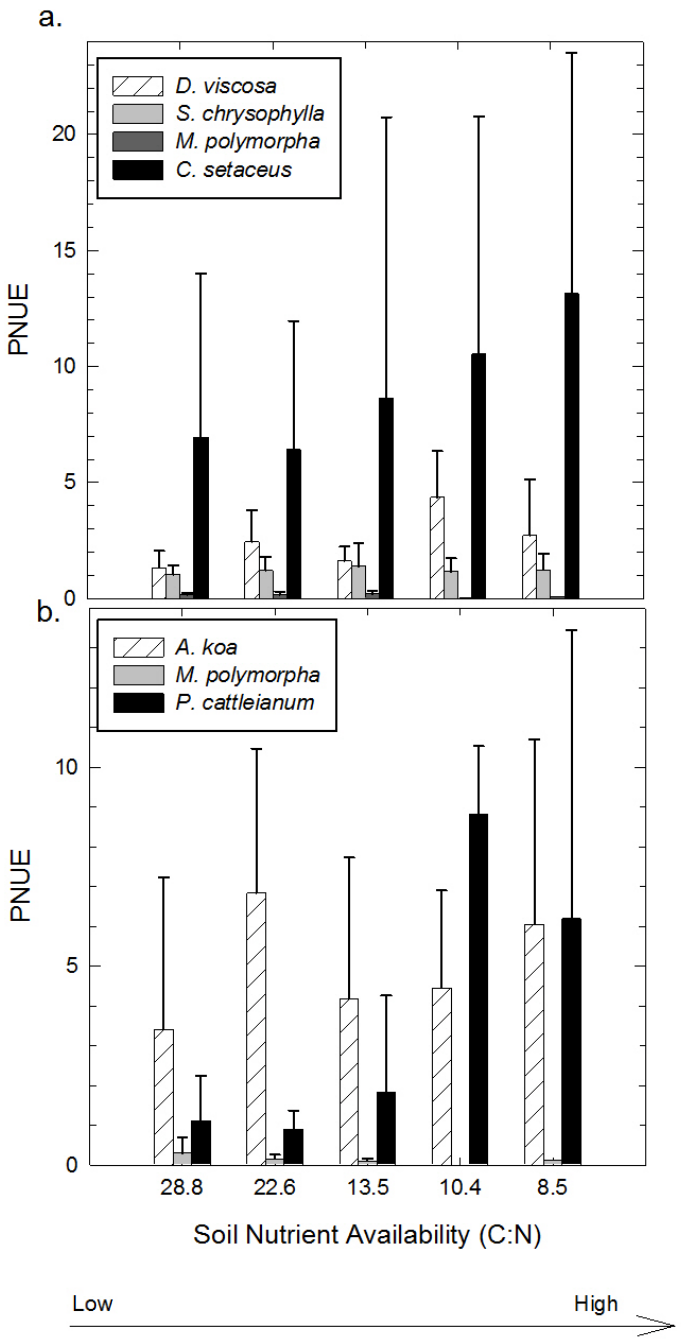

Figure 9. Mean photosynthetic nitrogen use efficiency (PNUE) for each species. PNUE response to changes in soil nutrient availability was significant for *P. cattleianum* only.

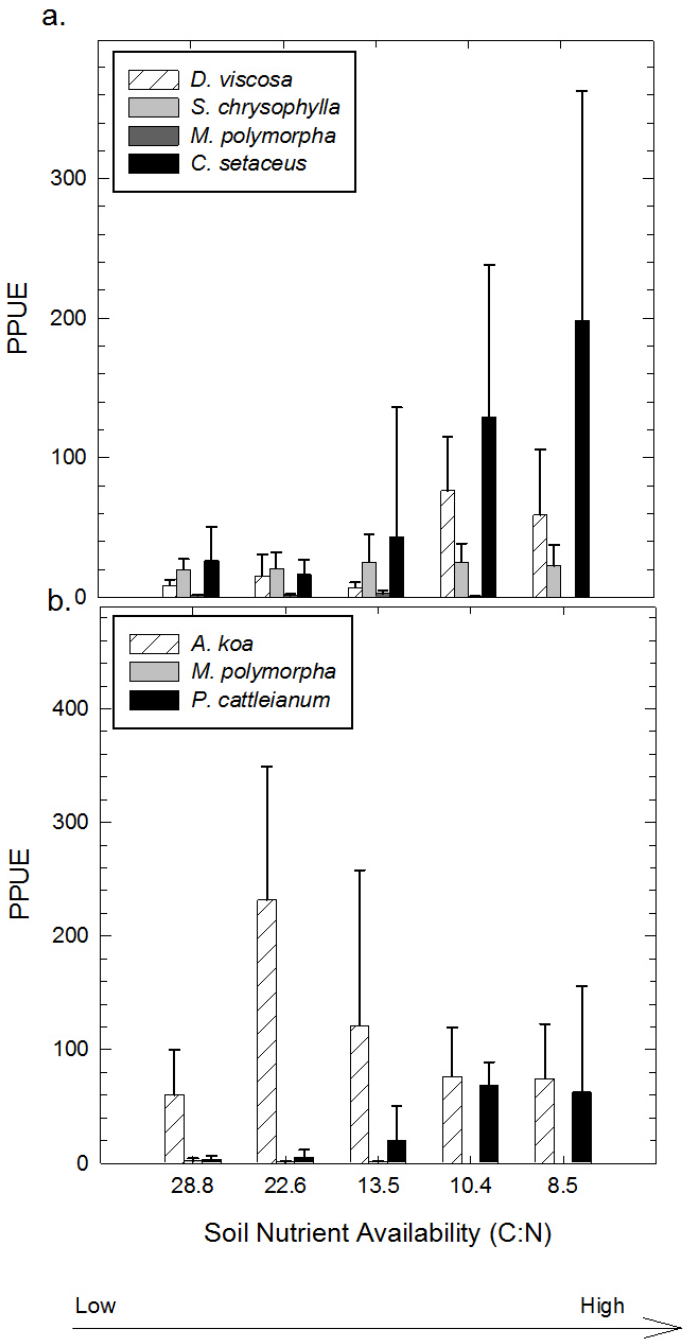

Figure 10. Mean photosynthetic phosphorus use efficiency (PPUE) for each species. PPUE response to changes in soil nutrient availability was significant for *D. viscosa, C. setaceus*, and *P. cattleianum*.

Discussion

Changes in nutrient cycling and nutrient availability can often facilitate the invasion of nonnative species (D'Antonio and Vitousek 1992, Ehrenfeld 2003, Foley et al. 2005). Many studies attempting to control invasive species do so by managing the plants themselves via top-down management activities (e.g., weeding, application of herbicides). However, manipulating the underlying drivers of invasion via bottom-up management (e.g., soil nutrient availability) is an alternative restoration and control strategy for invaded ecosystems. Decreasing soil nutrient levels via carbon amendments to give native species a competitive edge over invasive species has had mixed results in the literature (e.g. Allen and Zink 1998, Blumenthal 2009, Suding et al. 2004), and has not been examined in tropical systems or with woody species (Alpert 2010). Additionally, few studies have examined the effects of varying soil nutrient availability on both the growth and physiology of native and nonnative, invasive species. General differences in resource use strategy of native and invasive species (i.e., resource conservation vs. exploitation, respectively) are key to the success of nutrient manipulation as an ecological restoration technique. Therefore, this study examined the effect of varying soil nutrients on native vs. nonnative, invasive species, primarily woody species, present in Hawaiian tropical wet and dry ecosystems to address these current knowledge gaps.

Using dominant species from Hawaii's tropical wet and dry ecosystems, this study linked growth responses to nutrient manipulation with the underlying physiological mechanisms responsible for the growth responses observed. Linking growth and physiological responses allowed for an understanding of the resource use strategies that each species utilized to be successful. Generalities in exploitative resource use strategies were evident for both invasive species tested. However, the native species utilized displayed both resource conservation and resource exploitative strategies. Specifically for the native species tested, three of the four displayed no relationship between growth, photosynthetic parameters, and RUE with varying soil nutrient availability, indicating the utilization of resource conservation strategies typically associated with success in low nutrient environments. One native species, *D. viscosa*, responded to soil nutrient availability in the same manner as the nonnative, invasive species did by utilizing resource exploitative strategies (i.e., it displayed significant growth and photosynthetic responses to

changes in soil nutrients). *D. viscosa's* resource exploitative strategy likely explains its widespread presence in disturbed areas dominated by nonnative, invasive species, as well as its utility as a restoration species in highly disturbed areas.

Those species, which used resource exploitative strategies to be highly successful in high resource availability environments increased growth by utilizing extra nutrients to increase leaf area, not become more efficient. Native species, generally, were successful in low nutrient availability environments due to their efficient use of resources. Results from both the wet and dry ecosystems were the same in response to varying soil nutrients, where, in general, native species displayed resource conservative strategies and nonnative species displayed resource exploitative strategies. The similarity in responses of the dominant native and invasive species from two different ecosystem types suggests that these findings may be more widely applicable to different tropical ecosystems. Additionally, these results indicate that not all native species are resource conservative, and that understanding resource acquisition strategies of desired and unwanted species can help in informing management to promote desired species.

Growth responses

The original hypothesis that across tropical dry and wet ecosystem plants total biomass would increase with increasing soil nutrient availability was supported (Appendix D). Increases in biomass production from fertilization has been demonstrated in a variety of ecosystems (DiTommaso and Aarssen 1989), and was expected here. Prior studies on species responses to reduction of soil nutrient availability via carbon amendments have demonstrated that this technique generally decreases growth of both native and invasive species (Morghan and Seastedt 1999, Monaco et al. 2003, Suding et al. 2004, Gendron and Wilson 2007).

When individual species responses were examined, overall differences between native and invasive species were evident and in line with the original hypotheses for most, but not all, species. The hypothesis that native species would have a more neutral growth response to soil nutrient manipulations and invasive species would have a stronger response was partially supported. Three of the four native species – *A. koa*, *S. chrysophylla*, and *M. polymorpha* – responded as expected, with relatively consistent total biomass across

all soil nutrient treatments, suggesting the use of resource conservative strategies. In addition, *M. polymorpha* was negatively affected by increased nutrient availability, with average mortality between 79% and 92% in nutrient addition treatments across both ecosystem types. One native species, *D. viscosa* and both nonnative, invasive species responded with large increases in biomass with increasing soil nutrient availability, indicative of a resource exploitative strategy.

Native species, compared to nonnative, invasive species, often have adaptive fitness responses to varying resource availability which results in smaller decreases in fitness in response to environmental conditions such as nutrient availability (Davidson et al. 2011). The neutral growth response observed for the natives *A. koa, S. chrysophylla,* and *M. polymorpha* suggests that these species have adaptive fitness responses such as high RUE. The consistency in the response of *S. chrysophylla* and *A. koa* is also likely due to their ability to fix nitrogen when soil nutrients were reduced. The ideal response to carbon amendments is to favor native species by reducing the growth of invasive but not native species, or reducing growth in invasive more than native species. This ideal management scenario in line with the results presented here for these three native species (Horn and Redente 1998, Alpert and Maron 2000, Paschke et al. 2000). Additionally, native species adapted to low resource availability are often less able to take advantaged of increases in nutrients (Vitousek et al. 1987a, Hobbs and Huenneke 1996), explaining why even with large increases in nutrients, large increases in the total biomass for these three species was not observed. The results further suggest that increases in nutrients negatively affect survival of *M. polymorpha*, one of the most important canopy trees in native Hawaiian forests that also has high cultural and economical value. A prior field study examined the effects of fertilization on two montane wet forests in Hawaii and likewise found that growth and number of *M. polymorpha* seedlings was reduced when nutrients were added (Ostertag and Verville 2002a). Atmospheric N deposition and invasive N-fixing species are widespread phenomena globally that increase N availability (Vitousek and Walker 1989, Maron and Connors 1996, Wedin and Tilman 1996), and these results suggest that these elevated nutrient levels may negatively affect the regeneration of some native species, especially those adapted to low resource environments.

A single native species, *D. viscosa,* displayed responses similar to those of the invasive species and a resource exploitative strategy. The response of this native shrub suggests that its fast growth is due to traits of rapid resource uptake and utilization, making it an ideal and commonly used species for restoration of degraded habitats (Ammondt et al. 2013). Its ability to establish, grow quickly and provide shade also allows it to act as a nurse tree, providing a more suitable microclimate for native species establishment while reducing the cover of nonnative grasses (Santiago-García et al. 2008, Ammondt et al. 2013). It's resource exploitative strategy and adaptation to disturbances (Hodgkinson and Oxley 1990, D'Antonio et al. 2000, Ainsworth and Kauffman 2009) likely explains why it is commonly found in disturbed habitats dominated by invasive species.

High growth rates of invasive species often contribute to their success (Burns 2004, Garcia-Serrano et al. 2005, Burns 2006, Gurevitch et al. 2008), and are indicative of resource exploitative strategies, which is congruent with the observation that invasive species commonly invade areas of high resource availability (Burke and Grime 1996, Daehler 2003). Both *P. cattleianum* and *C. setaceus* displayed large increases in biomass with increasing soil nutrients, in line with these prior studies. Further, both invasive species exhibited large decreases in biomass when soil nutrients were reduced, and these results support several studies that have found carbon amendment to be successful at reducing invasive species biomass (Alpert and Maron 2000, Blumenthal et al. 2003). Further, reproduction of *C. setaceus* was inhibited by reductions in nutrient availability, with 80% of individuals in the high nutrient addition treatment producing inflorescences, compared to just 3% in the low nutrient reduction treatments. The reduction in *C. setaceus* reproductive output with lowered soil nutrients makes carbon amendments particularly useful for this aggressive invader, as the ability of a species to reproduce is critical to their success (Bryson and Carter 2004). Although we did not find that carbon amendments increased native species biomass as prior research has found (Allen and Zink 1998, Blumenthal et al. 2003, Perry et al. 2004, Prober et al. 2005a, Eschen et al. 2007), the reduction of invasive species biomass in response to carbon amendments is promising for restoration.

It was hypothesized that there would be no relationship between intraspecific competition and soil nutrient availability but that when species were in interspecific

competition increases in soil nutrient availability would increase differences in biomass (i.e., delta values) due to differences in resource use strategy of native and nonnative, invasive species. This hypothesis was only partially supported, as a relationship was found between soil nutrient availability and both intraspecific and interspecific competition for both invasive species. As soil nutrients increased, the delta (i.e., the difference in biomass of two species in a single pot) for interspecific competition increased as a result of the large increases in invasive species biomass while native species growth remained relatively constant. However, in nutrient reduction treatments the deltas of interspecific competition were smaller. This reaffirms the finding that the invasive species in our study utilize resource exploitative strategies while the native species, in general but not exclusively, use resource conservative strategies.

Photosynthetic capacity

Photosynthetic responses of all species mirrored the biomass responses. For all native species, except *D. viscosa*, whole plant carbon gain, G_s, and C_i responses to soil nutrient variations were neutral, as native species adapted to low resource environments were not negatively affected by decreases in soil nutrients and were unresponsive to the nutrient additions. Both invasive species and *D. viscosa* displayed strong responses to changes in soil nutrient availability, increasing rates of whole plant carbon gain when nutrient availability increased and decreasing whole plant carbon gain when nutrients were decreased. These results partially support the hypothesis that across all plants reduced nutrient availability would decrease photosynthesis but that invasive species would show stronger response to changes in nutrient availability than native species. These results further highlight the general differences in resource use strategies among the native species and invasive species. The consistent photosynthetic rates of most native species highlight their use resource conservative strategies, where invasive species large increase in photosynthetic rates when nutrients are added highlight their use of resource exploitative strategies. Prior research has found that high photosynthetic rates (Baruch and Goldstein 1999, McDowell 2002) is trait generally associated with plants that use resource exploitative strategies. In line with this prior research, when invasive and native species photosynthetic rates where compared, invasive species typically had higher photosynthetic

rates than native species (i.e., in nutrient rich environments). Nutrient reduction treatments for the resource exploitative species caused large decreases in whole plant carbon gain, inhibiting species overall growth. These results suggest that reductions in biomass of species that utilize resource exploitative strategies (i.e., invasive species), is linked to the affect of soil nutrient availability on plant photosynthetic rates.

Two parameters of photosynthesis, carboxylation capacity (V_{cmax}) and chloroplast electron transport capacity (J_{max}), were examined to determine if photosynthetic capacity was limited by soil nutrient availability. The hypothesis that V_{cmax} and J_{max} would be limited by soil nutrients and that invasive species would have higher rates of V_{cmax} and J_{max} was not supported. Prior research has shown V_{cmax} and J_{max} to be sensitive to reductions in soil nutrient availability (Zhang and Dang 2006), and that increases in nutrients, specifically nitrogen, can increase rates of V_{cmax} (Heberling and Fridley 2016). However, my results do not support these findings as rates of V_{cmax} and J_{max} did not change with soil nutrient availability.

Changes in photosynthetic efficiency, indicated by changes in V_{cmax} and J_{max}, may provide a mechanistic explanation for why a species is more successful. The results of this study, however, do not show plasticity of V_{cmax} and J_{max} in response to soil nutrient availability, suggesting that invasive species are more successful not because they become more efficient in photosynthesis with increasing soil nutrients, but rather because they use increased nutrient availability to increase their total leaf area, providing more surface area for photosynthesis and thus more biomass production. Native species were more successful in low resource environments as a result of more efficient use of resources.

Resource Use Efficiency

Prior studies have shown that having high or plastic RUE provides invasive species a competitive advantage over native species in resource poor environments (Funk and Vitousek 2007, Funk 2008, Davidson et al. 2011, Heberling and Fridley 2016, Sardans et al. 2016). In all but one case (i.e., PNUE of *C. setaceus*), PNUE and PPUE of invasive species were plastic in response to variation in soil nutrient availability. However, the plastically did not give invasive species an advantage over native species in the nutrient reduction treatments. These results are in line with the studies that found invasive species to

generally be more plastic than native species in RUE, but this plasticity didn't always result in improved fitness (Davidson et al. 2011). Additionally, my results support prior research that found invasive species to have lower RUE than native species in low resource environments (Peñuelas et al. 2010).

Native species RUE have been shown to be unresponsive to changes in soil nutrient availability (Davidson et al. 2011, Heberling and Fridley 2016). For three of the four native species our findings are consistent with these prior studies. *A. koa, S. chrysophylla,* and *M. polymorpha* all had constant RUE across all soil nutrient availability. However, in line with the biomass response, *D. viscosa* displayed the use of resource exploitative strategies with PPUE decreasing with decreasing soil nutrient availability. These findings only partially support the original hypothesis that RUE of native species would remain constant across nutrient levels and RUE of invasive species would be plastic, with RUE increasing with decreasing soil nutrient availability. However, these findings suggest that lowering resource availability may aid in the restoration of native species when native and invasive species resource use efficiencies differ (Funk 2013).

Ecosystem Comparisons and Field Implementation

Species utilized in this study are common to Hawaiian wet and dry ecosystems and are dominant components of the ecosystem in which they are present. I expected the response to soil nutrient manipulation of native and invasive species from both ecosystems to be similar, and they were. Similarities in response of wet and dry ecosystem species is a good indicator that soil nutrient manipulation may be used across different ecosystems and in various plant communities in tropical systems. My study was a greenhouse experiment in which many factors were controlled. Therefore application in the field is warranted to see if the patterns observed in the greenhouse hold. For example, in this greenhouse study water was not limiting, while in the field, especially in drier areas, the response to soil nutrient manipulation may be at least partially controlled by water availability. Those species better adapted to the present environmental conditions may be less affected by the soil nutrient manipulations regardless of their resource use strategies. Additionally, woody plants used for the greenhouse experiment were seedlings, and application of carbon amendments in mature plant communities may not affect established species as much as

recruitment and regeneration of new individuals. More complex plant competition may also cause differences in the outcome when soil nutrient manipulation is applied in the field, as species present at the time of implementation may affect the success of nutrient manipulation (Matzek 2011, Steers et al. 2011).

Conclusion

This study found that reduction in soil nutrient availability decreased total biomass and physiological traits (i.e., whole plant carbon gain) of two dominant Hawaiian invasive species, *C. setaceus* and *P. cattleianum*, as well as that of a single native species, *D. viscosa.* Three of four native species tested, in contrast, showed neutral responses to varying soil nutrient levels, with no differences in total biomass, whole plant carbon gain, G_s, C_i, or RUE. These results suggest that responses can be at least somewhat species-specific, and based on physiological traits that are not exclusive to native vs. invasive plants (i.e., at least some native species will behave more like invasive species based on their ecophysiology). The congruent response of invasive species (i.e., large increases in total biomass and whole plant carbon gain with increasing nutrients) was likely due to their utilization of a resource exploitative strategy, lack of phenotypic plasticity and resource conservative traits. Lack of plasticity in rates of V_{cmax} and J_{max} suggests that invasive species are successful in nutrient enriched environments not because they are more efficient but because they allocate additional nutrients to creating more plant material, specifically building more leaf area for photosynthesis. Response of the native shrub *D. viscosa* suggests that its fast growth may also be due to traits of rapid resource uptake and utilization, similar to those characteristics of invasive species, making it an ideal species for restoration projects in disturbed environments. The high mortality of *M. polymorpha* in nutrient addition treatments is attributed to its inability to tolerate pulses of nutrients. Collectively, the general responses of native and invasive species to variation in soil nutrients in this study support the use of soil nutrient manipulation as a restoration technique in Hawaiian wet and dry ecosystems, as well as other tropical ecosystems.

Decreasing soil nutrient availability, via carbon amendments, can reduce the growth of invasive species (e.g. Allen and Zink 1998, Perry et al. 2004), giving native species a chance to recover in invaded ecosystems. This study shows that the invasive species used

resource exploitative strategies and that almost all native species used resource conservative strategies, making soil nutrient manipulation an ideal method for the restoration of invaded ecosystems. Numerous factors were controlled in this greenhouse experiment that have the ability to change the outcome of results when applied in a natural setting. Studies have shown that community structure, environmental variables, plant traits, and restoration implementation timing can affect the outcome of soil nutrient manipulation (Matzek 2011, Steers et al. 2011). Based on the results of the current and prior studies, recommendations for restoration of invaded wet and dry Hawaiian ecosystems include application of carbon amendments in areas where invasive species present have been shown to utilize resource exploitative strategies and desired native species utilize resource conservative strategies.

Chapter 3

Conclusion

Invasive species are a major component of environmental change and threaten native ecosystems globally. Understanding how resource availability can impact invasive species is an important area for research and may influence restoration of invaded ecosystems. Prior research has shown that reducing soil nutrient availability can reduce the abundance of invasive species, giving native species a competitive edge, especially in systems where native species are adapted to low resource availability (Alpert and Maron 2000, Blumenthal et al. 2003, Alpert 2010). Conversely, increasing soil nutrient availability typically favors invasive species, especially those who utilize resource exploitative strategies to succeed (Ostertag and Verville 2002b, Blumenthal et al. 2003). However, the effect of varying soil nutrients on the competitive dynamics between native and invasive species in tropical systems and for woody species is largely untested (Alpert 2010). Additionally, to date, many studies that have investigated the effects of decreasing soil nutrient availability as a restoration tool have not done so in the context of resource use efficiency (RUE).

This study found that reduction in soil nutrient availability inhibits increases in total biomass and physiological traits (whole plant carbon gain) of two dominant Hawaiian invasive species, *C. setaceus* and *P. cattleianum*, as well as that of a single native species, *D. viscosa.* Three of the four native species tested, in contrast, showed neutral responses to varying soil nutrient levels, with no differences in total biomass, whole plant carbon gain, G_s, C_i, or RUE. These results suggest that responses can be species specific, and based on physiological traits that vary across native and invasive plants. The congruent response of invasive species (i.e., large increases in total biomass and whole plant carbon gain with increasing nutrients) was likely due to their utilization of a resource exploitative strategy, and lack of phenotypic plasticity. Lack of plasticity in rates of V_{cmax} and J_{max} suggests that invasive species are successful in nutrient enriched environments not because they are more efficient but because they allocate additional nutrients to creating more leaf area for photosynthesis. Response of the native shrub *D. viscosa* suggests that its fast growth may also be due to traits of rapid resource uptake and utilization, similar to those

characteristics of invasive species, making it an ideal species for restoration projects in disturbed environments. The high mortality of *M. polymorpha* in nutrient addition treatments is attribute to its inability to tolerate pulses of high nutrients. Additionally, the neutral response of *S. chrysophylla* and *A. koa* is likely credited to their ability to fix nitrogen and the native species inability to utilize additional resources. Collectively, the general responses of native and invasive species to variation in soil nutrients support the use of soil nutrient manipulation as a restoration technique in Hawaiian wet and dry ecosystems.

My study suggests that with careful planning and prior knowledge of species traits, soil nutrient manipulation may be used to restore invaded ecosystems. Field trails should be carried out to further understanding of soil nutrient manipulation as a restoration technique. This greenhouse study was highly controlled and utilized plant seedlings. Therefore, application in a natural setting with plants of various ages may alter the outcome of soil nutrient manipulation. A field trial can address the complexities not explored in the greenhouse and provide insight into soil nutrient manipulation as a feasible restoration method.

Appendix A

Plant sources

Table A 1. Source of species used in the greenhouse experiment.

Species	Seedling Source
Dodonaea viscosa and *S. chrysophylla*	Native Nursery, LLC; Maui
M. polymorpha	Institute of Pacific Island Forestry (IPIF); Island of Hawaii
A. koa	Aileen's Nursery; Island of Hawaii
P. cattleianum	Local stands, behind IPIF; Island of Hawaii
C. setaceus	Study site off of Saddle Road; Island of Hawaii

Appendix B

Initial substrate conditions & soil nutrient availability treatments

Table B 1. Amount of soil, sucrose, sawdust, and fertilizer added to eat pot for each nutrient manipulation treatment.

Treatment	Pot Contents
Control	~3.14 kg soil
Nutrient Reduction – High	220 g sawdust + 220 g sucrose + ~3.14 kg soil
Nutrient Reduction – Low	70 g sawdust + 70 g sucrose +~3.14 kg soil
Nutrient Addition - High	30 g of Apex 16-6-12 NPK fertilizer + ~3.14 kg soil
Nutrient Addition – Low	15 g of Apex 16-6-12 NPK fertilizer + ~3.14 kg soil

Table B 2. Initial carbon and nitrogen content in the different substrates used. These values were used to determine the quantity of carbon additions needed to obtain the target C:N ratios.

	C:N	%C	%N
Soil	13.5	3.7	.27
Sawdust	236.1	48.4	.21
Sucrose	691.8	42.2	.06

Appendix C

Initial Plant Conditions

Foliar Nutrient/Isotope Samples

Baseline foliar samples were taken from leftover individuals not used in the study and analyzed for % P, C, and N, and $\delta^{13}C$ and $\delta^{15}N$. Leaves were collected from multiple seedlings to obtain the mass necessary to run six replicates. There was not enough leftover *M. polymorpha* and *P. cattleianum* materials to analyze six samples, so fewer samples were run for these species (Table C1). Samples were sent to the University of Hawaii Analytical Lab (UHHAL - %P, C, and N) and Cornell Isotope Laboratory (COIL - $\delta^{13}C$ and $\delta^{15}N$) for analyses. Results from initial nutrient analyses of all plants showed low coefficient of variation (Table C1), confirming homogeneity of plants prior to treatment application.

Table C 1. The average foliar nutrient content for each plant (1 S.D.). Initial nutrient analyses for all species confirmed homogeneity of plants prior to treatment application.

Plant Species	**n**	**%N (S.D.)**	**$\delta^{15}N$, (S.D.)**	**%C. (S.D.)**	**$\delta^{13}C$, (S.D.)**	**%P, (S.D.)**
A. koa	6	2.47, (0.19)	0.48, (0.22)	47.93, (0.60)	-31.52, (-0.53)	0.36, (0.02)
C. setaceus	6	1.85, (0.19)	4.04, (0.97)	40.66, (0.86)	-12.25, (0.22)	0.21, (0.03)
M. polymorpha	4	1.54, (0.05)	-0.74, (0.25)	48.47, (0.63)	-29.08, (0.26)	0.14, (0.01)
D. viscosa	6	1.46, (0.13)	0.24, (0.22)	47.79, (1.59)	-30.45, (0.59)	0.15, (0.02)
S. chrysophylla	6	2.41, (0.30)	-0.31, (0.35)	48.05, (1.28)	-32.01, (0.43)	0.22, (0.02)
P. cattleianum	3	0.79, (0.13)	-4.86, (1.03)	46.31, (0.39)	-31.60, (0.26)	0.09, (0.03)

Plant Size

Initial plant measurements (height, basal diameter, canopy cover for all species except *C. setaceus* individuals, which were weighed because of propagation method) were taken to ensure homogeneity in initial sizes across species and treatments. While plants were randomly applied to treatments, posterior analyses of plant measurements showed that initial plant size differed across treatments for all species except *C. setaceus* (Tables C2-C5).

Table C 2. The P value and F ratio for each species from the ANOVA testing differences in baseline measurements across nutrient availability treatments in the dry ecosystem (n=120 for all species except *C. setaceus* where n=200). Significant differences at α = 0.05 indicated with *italicized* P values.

Species	Height	Basal Diameter	Canopy Cover	Weight
D. viscosa	*<0.01* 7.8	*<0.01*, 15.8	*<0.01*, 6.1	-
C. setaceus	-	-	-	0.17, 1.6
M. polymorpha	0.05, 2.4	*<0.01*, 3.7	*<0.01*, 4.5	-
S. chrysophylla	*0.01*, 3.4	*<0.01*, 13.1	0.14, 1.8	-

Table C 3. The mean (1 S.D.) of each baseline measurement taken at the beginning of the experiment for each species and treatment in the dry ecosystem (n=120 for all species except *C. setaceus* where n=200). Superscript letters indicate significant differences in baseline conditions.

Species	Treatment	Mean Canopy Cover (cm)	Mean Height (cm)	Mean Basal Diameter (cm)	Weight (g)
C. setaceus	(-/-)	-	-	-	^{A}5.05, (2.32)
C. setaceus	(-)	-	-	-	^{A}4.79, (3.37)
C. setaceus	(o)	-	-	-	^{A}3.87, (1.53)
C. setaceus	(+)	-	-	-	^{A}4.30, (1.56)
C. setaceus	(+/+)	-	-	-	^{A}3.88, (1.09)
D. viscosa	(-/-)	^{A}19.05, (3.58)	^{A}28.33, (7.48)	^{A}0.30, (0.06)	-
D. viscosa	(-)	^{B}22.26, (4.44)	^{BC}39.37, (10.9)	^{B}0.30, (0.05)	-
D. viscosa	(o)	^{AB}21.36, (2.68)	^{AB}31.86, (9.69)	^{AB}0.30, (0.05)	-
D. viscosa	(+)	^{B}24.05, (4.22)	^{C}41.58, (8.91)	^{B}0.30, (0.06)	-
D. viscosa	(+/+)	^{B}22.78, (3.58)	^{C}40.66, (7.85)	^{C}0.30, (0.05)	-
M. polymorpha	(-/-)	^{A}3.00, (0.75)	^{A}3.87, (1.64)	^{AB}0.10, (0.02)	-
M. polymorpha	(-)	^{AB}3.69, (1.08)	^{A}4.24, (1.43)	^{B}0.12, (0.04)	-
M. polymorpha	(o)	^{B}3.96, (1.20)	^{A}5.08, (1.81)	^{B}0.11, (0.04)	-
M. polymorpha	(+)	^{B}4.28, (1.36)	^{A}5.10, (1.81)	^{B}0.11, (0.02)	-
M. polymorpha	(+/+)	^{B}3.90, (1.10)	^{A}4.36, (1.94)	^{A}0.09, (0.05)	-
S. chrysophylla	(-/-)	^{A}21.67, (3.61)	^{A}36.51, (8.03)	^{A}0.36, (0.04)	-
S. chrysophylla	(-)	^{A}22.13, (3.62)	^{AB}37.10, (6.79)	^{B}0.35, (0.03)	-
S. chrysophylla	(o)	^{A}23.94, (3.17)	^{AB}56.17, (8.55)	^{B}0.31, (0.03)	-
S. chrysophylla	(+)	^{A}22.25, (4.33)	^{B}42.91, (5.67)	^{B}0.37, (0.03)	-
S. chrysophylla	(+/+)	^{A}21.11, (3.49)	^{AB}41.16, (7.75)	^{B}0.38, (0.05)	-

Table C 4. The P value and F ratio for each species from the ANOVA testing differences in baseline measurements among treatments in the wet ecosystem (n=120 for all species except *P. cattleianum* where n=160). Significant differences at α = 0.05 indicated with *italicized* P values.

Species	Height	Basal Diameter	Canopy Cover
A. koa	*<0.01*, 13.7	*<0.01*, 12.1	*<0.01*, 8.6
M. polymorpha	*<0.01*, 4.1	*0.01*, 3.4	*<0.01*, 8.6
P. cattleianum	*0.02*, 3.1	0.28, 1.3	0.24, 1.4

Table C 5. The mean (1 S.D.) of each baseline measurement taken at the beginning of the experiment for each species and treatment in the wet ecosystem (n=120 for all species except *P. cattleianum* where n=160). Superscript letters indicate significant differences in baseline conditions.

Species	Treatment	Mean Canopy Cover (cm)	Mean Height (cm)	Mean Basal Diameter (cm)
A. koa	(-/-)	^{A}15.78, (5.01)	^{AB}15.74, (5.23)	^{A}0.17, (0.03)
A. koa	(-)	^{AB}13.99, (5.97)	^{BC}13.86, (7.74)	^{A}0.17, (0.05)
A. koa	(o)	^{A}16.76, (5.69)	^{A}17.86, (6.75)	^{A}0.20, (0.48)
A. koa	(+)	^{C}9.52, (1.63)	^{D}8.49, (1.89)	^{B}0.13, (0.02)
A. koa	(+/+)	^{BC}10.69, (2.06)	^{CD}9.33, (2.66)	^{B}0.14, (0.02)
M. polymorpha	(-/-)	^{A}2.74, (0.92)	^{A}3.48, (1.22)	^{A}0.08, (0.02)
M. polymorpha	(-)	^{AB}3.16, (0.93)	^{A}3.37, (1.35)	^{A}0.10, (0.03)
M. polymorpha	(o)	^{A}2.82, (0.95)	^{AB}3.86, (2.00)	^{A}0.10, (0.02)
M. polymorpha	(+)	^{C}4.25, (1.66)	^{B}5.05, (2.02)	^{A}0.11, (0.05)
M. polymorpha	(+/+)	^{BC}3.89, (1.15)	^{AB}4.20, (1.45)	^{A}0.08, (0.02)
P. cattleianum	(-/-)	^{A}5.24, (1.70)	^{AB}10.69, (3.17)	^{A}0.12, (0.03)
P. cattleianum	(-)	^{A}4.76, (1.35)	^{AB}9.34, (2.70)	^{A}0.11, (0.02)
P. cattleianum	(o)	^{A}4.58, (1.27)	^{B}8.96, (2.75)	^{A}0.10, (0.01)
P. cattleianum	(+)	^{A}4.64, (1.53)	^{AB}9.66, (3.38)	^{A}0.11, (0.03)
P. cattleianum	(+/+)	^{A}5.15, (1.57)	^{A}11.71, (4.66)	^{A}0.11, (0.03)

Appendix D

Additional Analysis

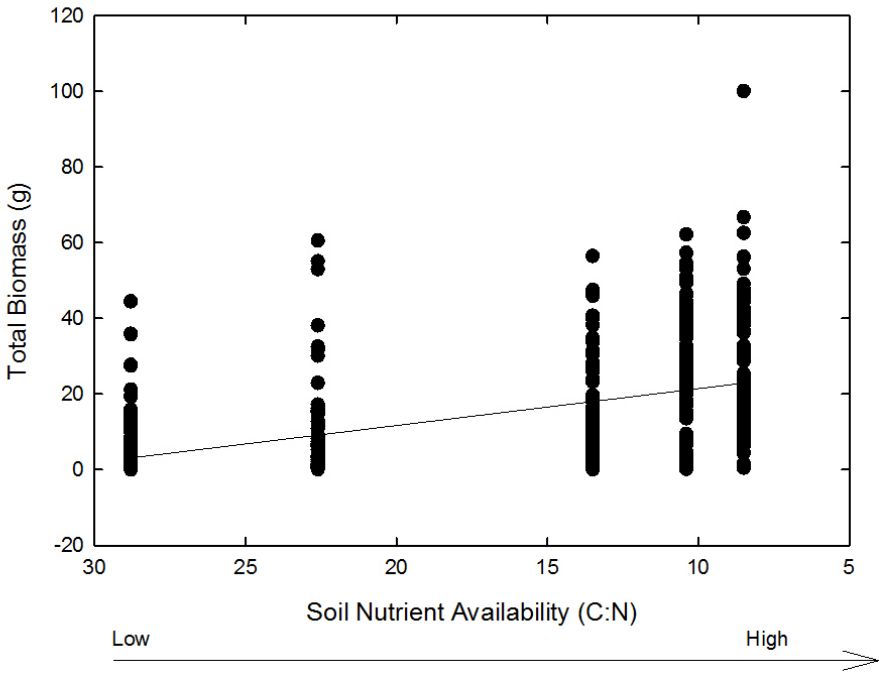

Figure D 1. Total biomass for all species grown across varying soil nutrient availabilities. Regression line illustrates significant relationship observed of increases in total biomass with increasing soil nutrients.

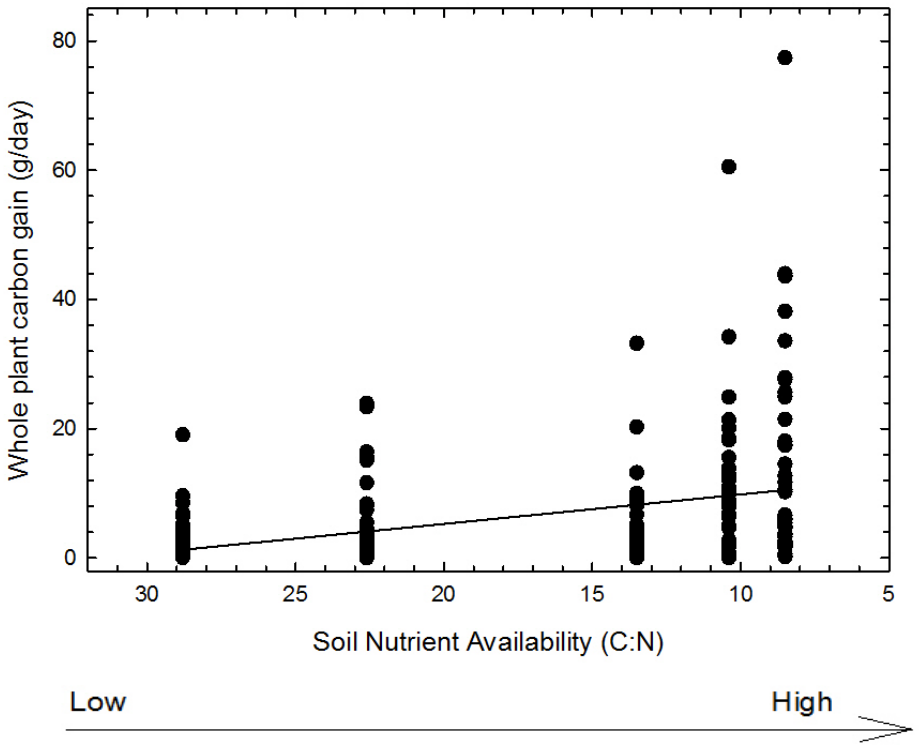

Figure D 2. Whole plant carbon gain for all species grown across varying soil nutrient availabilities. Regression line illustrates significant relationship bewteen plant carbon gain and soil nutrient availability

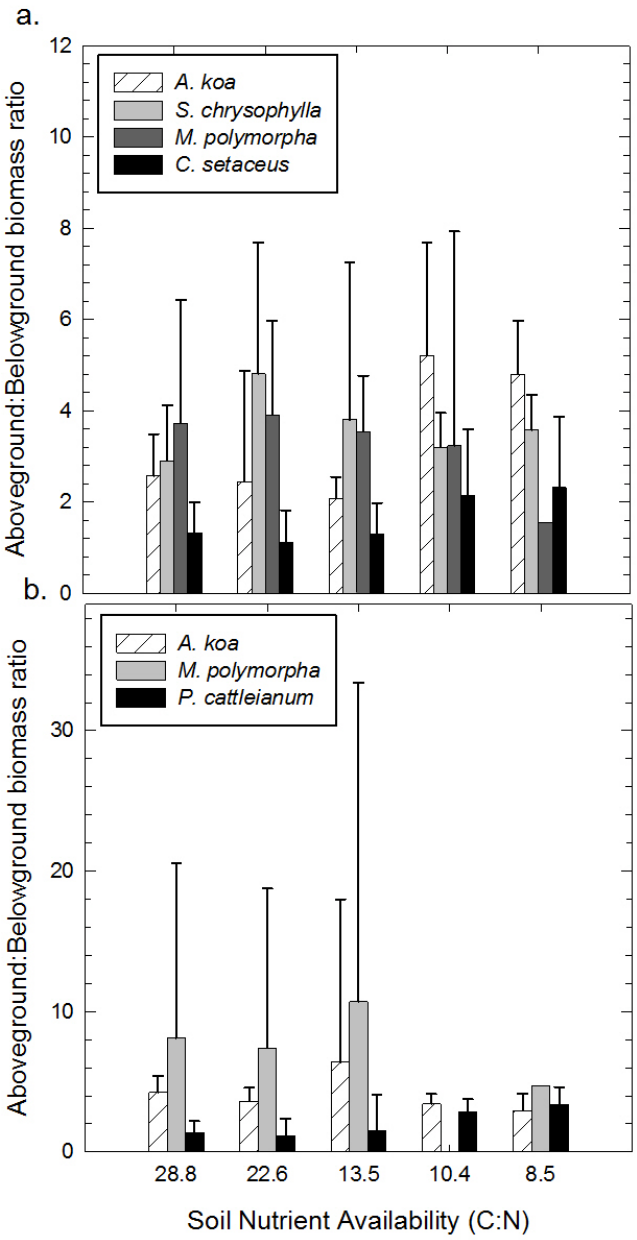

Figure D 3. Mean aboveground: belowground biomass ratio for the dry (a) and wet (b) ecosystem across soil nutrient availability. Significant relationships between soil nutrient availability and aboveground:belowground biomass were found for *D. viscosa*, *C. setaceus,* and *P. cattleianum.*

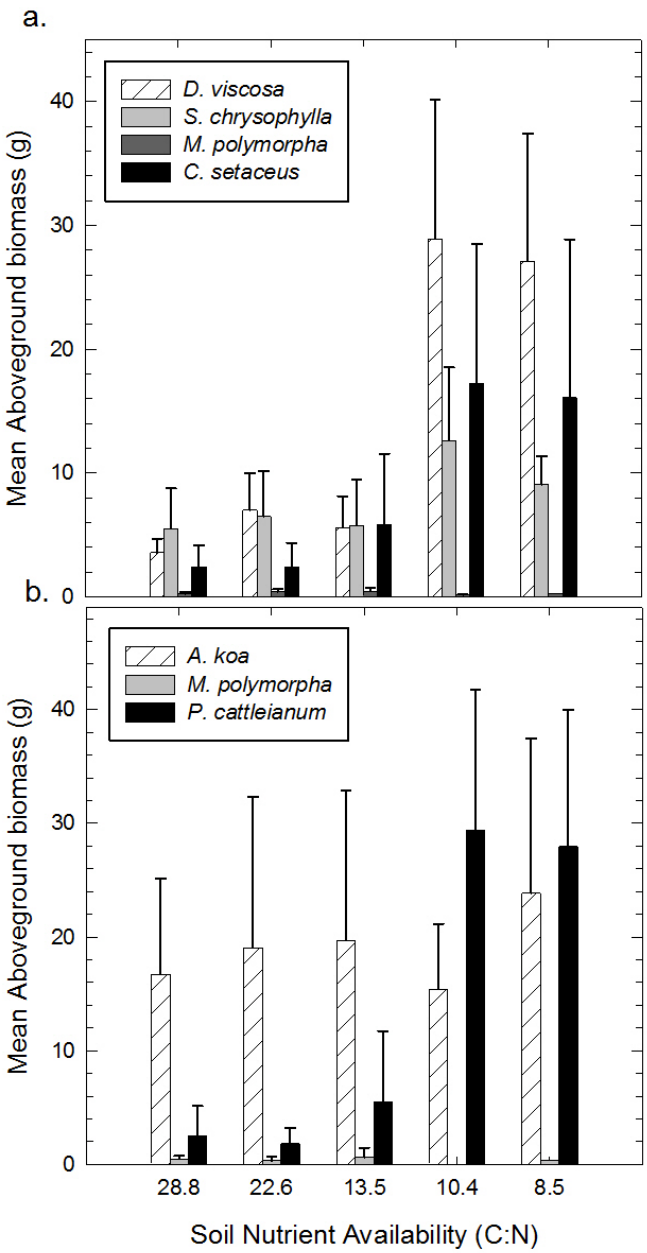

Figure D 4. Mean aboveground biomass ratio for the dry (a) and wet (b) ecosystems across soil nutrient availability. Significant relationships between soil nutrient availability and aboveground biomass were found for *D. viscosa*, *C. setaceus, S. chrysophylla* and *P. cattleianum.*

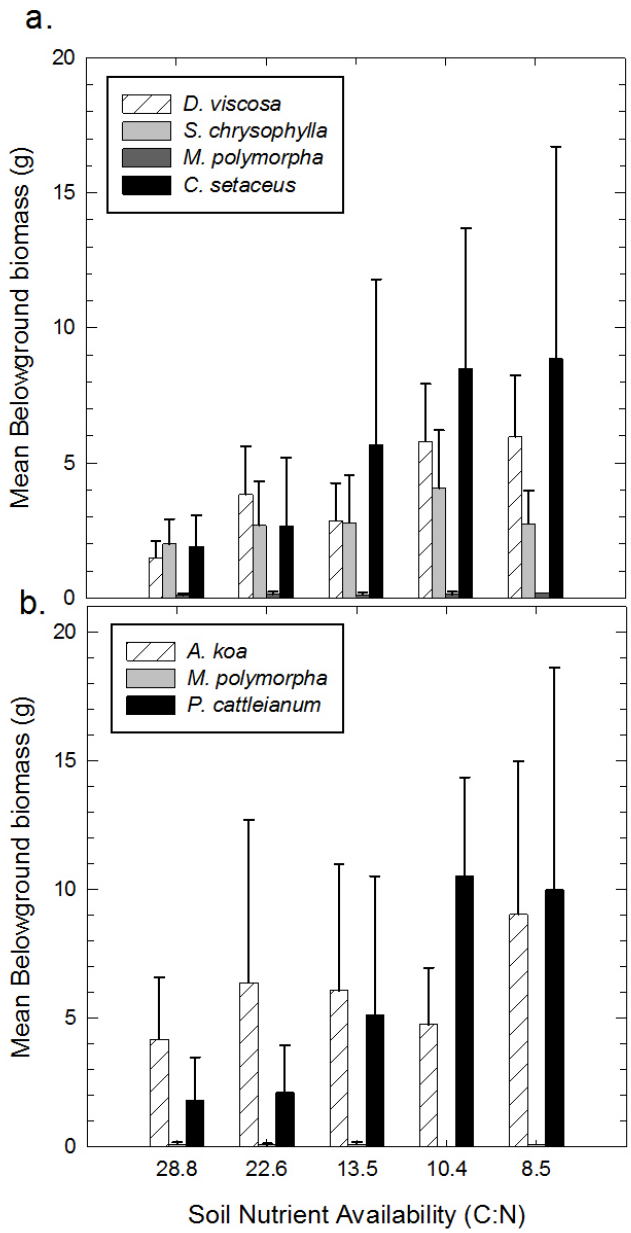

Figure D 5. Mean belowground biomass ratio for the dry (a) and wet (b) ecosystems across soil nutrient availability. Significant relationships between soil nutrient availability and belowground biomass were found for *D. viscosa*, *C. setaceus, S. chrysophylla* and *P. cattleianum.*

Literature Cited

Ainsworth, A., and J. B. Kauffman. 2009. Response of native Hawaiian woody species to lava-ignited wildfires in tropical forests and shrublands. Plant Ecology **201**:197-209.

Allen, M. F., and T. A. Zink. 1998. The effects of organic amendments on the restoration of a disturbed coastal sage scrub habitat. Restoration Ecology **6**:52-58.

Alpert, P. 2010. Amending invasion with carbon: after fifteen years, a partial success. Rangelands **32**:12-15.

Alpert, P., E. Bone, and C. Holzapfel. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in plant ecology, evolution and systematics **3**:52-66.

Alpert, P., and J. L. Maron. 2000. Carbon addition as a countermeasure against biological invasion by plants. Biological Invasions **2**:33-40.

Ammondt, S., C. Litton, L. Ellsworth, and J. Leary. 2013. Restoration of native plant communities in a Hawaiian dry lowland ecosystem dominated by the invasive grass Megathyrsus maximus. Applied Vegetation Science **16**:29-39.

Anderson, S. J., and C. P. Stone. 1993. Snaring to control feral pigs Sus scrofa in a remote Hawaiian rain forest. Biological Conservation **63**:195-201.

Banko, P. C., S. C. Hess, P. G. Scowcroft, C. Farmer, J. D. Jacobi, R. M. Stephens, R. J. Camp, D. L. Leonard Jr, K. W. Brinck, and J. Juvik. 2014. Evaluating the Long-Term Management of Introduced Ungulates to Protect the Palila, an Endangered Bird, and Its Critical Habitat in Subalpine Forest of Mauna Kea, Hawai'i. Arctic, Antarctic, and Alpine Research **46**:871-889.

Baruch, Z., and G. Goldstein. 1999. Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. Oecologia **121**:183-192.

Bleier, J. S., and R. D. Jackson. 2007. Manipulating the quantity, quality, and manner of C addition to reduce soil inorganic N and increase C4: C3 grass biomass. Restoration Ecology **15**:688-695.

Blumenthal, D. 2009. Carbon addition interacts with water availability to reduce invasive forb establishment in a semi-arid grassland. Biological Invasions **11**:1281-1290.

Blumenthal, D., N. Jordan, and M. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. Ecological Applications **13**:605-615.

Bruegmann, M. M. 1996. Hawaii's dry forests. Endangered Species Bulletin **21**:26-27.

Bryson, C. T., and R. Carter. 2004. Biology of Pathways for Invasive Weeds 1. Weed Technology **18**:1216-1220.

Bullock, D., S. North, M. Dulloo, and M. Thorsen. 2002. The impact of rabbit and goat eradication on the ecology of Round Island, Mauritius. Turning the tide: the eradication of invasive species:53-63.

Burke, I., E. Bontti, J. Barrett, P. Lowe, W. Lauenroth, and R. Riggle. 2013. Impact of labile and recalcitrant carbon treatments on available nitrogen and plant communities in a semiarid ecosystem. Ecological Applications **23**:537-545.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77**:776-790.

Burns, J. H. 2004. A comparison of invasive and non-invasive dayflowers (Commelinaceae) across experimental nutrient and water gradients. Diversity and Distributions **10**:387-397.

Burns, J. H. 2006. Relatedness and environment affect traits associated with invasive and noninvasive introduced Commelinaceae. Ecological Applications **16**:1367-1376.

Cabin, R., S. Weller, D. Lorence, S. Cordell, and L. Hadway. 2002a. Effects of microsite, water, weeding, and direct seeding on the regeneration of native and alien species within a Hawaiian dry forest preserve. Biological Conservation **104**:181-190.

Cabin, R., S. Weller, D. Lorence, S. Cordell, L. Hadway, R. Montgomery, D. Goo, and A. Urakami. 2002b. Effects of light, alien grass, and native species additions on Hawaiian dry forest restoration. Ecological Applications **12**:1595-1610.

Cabin, R., S. Weller, D. Lorence, T. Flynn, A. Sakai, D. Sandquist, and L. Hadway. 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. Conservation Biology **14**:439-453.

Carlquist, S. 1974. Island biology. Columbia University Press: New York & London. 660pp **581**:5279.

Chapin, F. S. 1980. The mineral nutrition of wild plants. Annual review of ecology and systematics **11**:233-260.

Cione, N. K., P. E. Padgett, and E. B. Allen. 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. Restoration Ecology **10**:376-384.

Cole, R., and C. Litton. 2014. Vegetation response to removal of non-native feral pigs from Hawaiian tropical montane wet forest. Biological Invasions **16**:125-140.

Coley, P. D., J. P. Bryant, and F. S. Chapin III. 1985. Resource availability and plant antiherbivore defense. Science(Washington) **230**:895-899.

Corbin, J. D., and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology **85**:1273-1283.

Cordell, S., R. Ostertag, B. Rowe, L. Sweinhart, L. Vasquez-Radonic, J. Michaud, T. Cole, and J. Schulten. 2009. Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest. Biological Conservation **142**:2997-3004.

Cordell, S., and D. Sandquist. 2008. The impact of an invasive African bunchgrass (Pennisetum setaceum) on water availability and productivity of canopy trees within a tropical dry forest in Hawaii. Functional Ecology **22**:1008-1017.

Courchamp, F., J.-L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews **78**:347-383.

Cuddihy, L. W., and C. P. Stone. 1990. Alteration of native Hawaiian vegetation: Effects of humans, their activities and introductions. Cooperative National Park Resources Studies Unit, University of Hawaii at Manoa, Hawaii, USA.

Cushman, J. H., T. A. Tierney, and J. M. Hinds. 2004. Variable effects of feral pig disturbances on native and exotic plants in a California grassland. Ecological Applications **14**:1746-1756.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual review of ecology and systematics **23**:63-87.

D'Antonio, C. M. 2000. Fire, plant invasions, and global changes. Island Press, Washington, DC.

D'Antonio, C. M., J. T. Tunison, and R. K. Loh. 2000. Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. Austral Ecology **25**:507-522.

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. Annual Review of Ecology, Evolution, and Systematics **34**:183-211.

Davidson, A. M., M. Jennions, and A. B. Nicotra. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology letters **14**:419-431.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

Denslow, J. S. 2003. Weeds in paradise: thoughts on the invasibility of tropical islands. Annals of the Missouri Botanical Garden:119-127.

DiTommaso, A., and L. Aarssen. 1989. Resource manipulations in natural vegetation: a review. Vegetatio **84**:9-29.

Donlan, C. J., B. R. Tershy, and D. A. Croll. 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation. Journal of Applied Ecology **39**:235-246.

Durand, L. Z., and G. Goldstein. 2001. Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. Oecologia **126**:345-354.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems **6**:503-523.

Eschen, R., S. R. Mortimer, C. S. Lawson, A. R. Edwards, A. J. Brook, J. M. Igual, K. Hedlund, and U. Schaffner. 2007. Carbon addition alters vegetation composition on ex-arable fields. Journal of Applied Ecology **44**:95-104.

Eschen, R., H. Muller-Scharer, and U. Schaffner. 2006. Soil carbon addition affects plant growth in a species-specific way. Journal of Applied Ecology **43**:35-42.

Field, C., and H. A. Mooney. 1986. The photosynthesis-nitrogen relationships in wild plants. Pages 25-55 *in* T. J. Givinish, editor. On the economy of plant form and function. Cambridge University Press, Cambridge.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, and H. K. Gibbs. 2005. Global consequences of land use. Science **309**:570-574.

Funk, J. L. 2008. Differences in plasticity between invasive and native plants from a low resource environment. Journal of Ecology **96**:1162-1173.

Funk, J. L. 2013. The physiology of invasive plants in low-resource environments. Conservation Physiology **1**:cot026.

Funk, J. L., and P. M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature **446**:1079-1081.

Gallardo, A., and W. H. Schlesinger. 1995. Factors determining soil microbial biomass and nutrient immobilization in desert soils. Biogeochemistry **28**:55-68.

Garcia-Serrano, H., J. Escarré, É. Garnier, and F. X. Sans. 2005. A comparative growth analysis between alien invader and native Senecio species with distinct distribution ranges. Ecoscience **12**:35-43.

Gendron, F., and S. D. Wilson. 2007. Responses to fertility and disturbance in a low-diversity grassland. Plant Ecology **191**:199-207.

Gimeno, I., M. Vila, and P. E. Hulme. 2006. Are islands more susceptible to plant invasion than continents? A test using Oxalis pes-caprae L. in the western Mediterranean. Journal of Biogeography **33**:1559-1565.

González, A. L., J. S. Kominoski, M. Danger, S. Ishida, N. Iwai, and A. Rubach. 2010. Can ecological stoichiometry help explain patterns of biological invasions? Oikos **119**:779-790.

Grotkopp, E., and M. Rejmánek. 2007. High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. American Journal of Botany **94**:526-532.

Gurevitch, J., T. G. Howard, I. W. Ashton, E. A. Leger, K. M. Howe, E. Woo, and M. Lerdau. 2008. Effects of experimental manipulation of light and nutrients on establishment of seedlings of native and invasive woody species in Long Island, NY forests. Biological Invasions **10**:821-831.

Heberling, J. M., and J. D. Fridley. 2016. Invaders do not require high resource levels to maintain physiological advantages in a temperate deciduous forest. Ecology **97**:874-884.

Hobbs, R. J., and L. F. Huenneke. 1996. Disturbance, diversity, and invasion: implications for conservation. Pages 164-180 Ecosystem Management. Springer.

Hodgkinson, K., and R. Oxley. 1990. Influence of fire and edaphic factors on germination of the arid zone shrubs Acacia aneura, Cassia nemophila and Dodonaea viscosa. Australian Journal of Botany **38**:269-279.

Horn, B. E., and E. F. Redente. 1998. Soil nitrogen and plant cover of an old-field on the shortgrass steppe in southeastern Colorado. Arid Land Research and Management **12**:193-206.

Lambers, H., and H. Poorter. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences.

Laungani, R., and J. M. Knops. 2009. Species-driven changes in nitrogen cycling can provide a mechanism for plant invasions. Proceedings of the National Academy of Sciences **106**:12400-12405.

Litton, C. M., D. R. Sandquist, and S. Cordell. 2006. Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. Forest Ecology and Management **231**:105-113.

Litton, C. M., D. R. Sandquist, and S. Cordell. 2008. A non-native invasive grass increases soil carbon flux in a Hawaiian tropical dry forest. Global Change Biology **14**:726-739.

Loope, L., and A. Medeiros. 1994. Impacts of biological invasions on the management and recovery of rare plants in Haleakala National Park, Maui, Hawaiian Islands.

Maron, J. L., and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. Oecologia **105**:302-312.

Matzek, V. 2011. Superior performance and nutrient-use efficiency of invasive plants over non-invasive congeners in a resource-limited environment. Biological Invasions **13**:3005-3014.

McDowell, S. C. L. 2002. Photosynthetic characteristics of invasive and noninvasive species of Rubus (Rosaceae). American Journal of Botany **89**:1431-1438.

Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of Intermountain West grasses to soil nitrogen. Journal of Range Management:282-290.

Morghan, K., and T. Seastedt. 1999. Effects of soil nitrogen reduction on nonnative plants in restored grasslands. Restoration Ecology **7**:51-55.

O'Dowd, D. J., P. T. Green, and P. S. Lake. 2003. Invasional 'meltdown' on an oceanic island. Ecology letters **6**:812-817.

Oduor, A. M., J. M. Gómez, and S. Y. Strauss. 2010. Exotic vertebrate and invertebrate herbivores differ in their impacts on native and exotic plants: a meta-analysis. Biological Invasions **12**:407-419.

Ostertag, R., and J. Verville. 2002a. Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests. Plant Ecology **162**:77-90.

Ostertag, R., and J. H. Verville. 2002b. Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests. Plant Ecology **162**:77-90.

Pammenter, N., P. M. Drennan, and V. Smith. 1986. PHYSIOLOGICAL AND ANATOMICAL ASPECTS OF PHOTOSYNTHESIS OF TWO AGROSTIS SPECIES AT A SUB-ANTARCTIC ISLAND. New Phytologist **102**:143-160.

Parker, J. D., D. E. Burkepile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. Science **311**:1459-1461.

Paschke, M. W., T. McLendon, and E. F. Redente. 2000. Original articles: nitrogen availability and old-field succession in a shortgrass steppe. Ecosystems **3**:144-158.

Pattison, R. R., G. Goldstein, and A. Ares. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia **117**:449-459.

Paulay, G. 1994. Biodiversity on oceanic islands: its origin and extinction1. American Zoologist **34**:134-144.

Pavlik, B. M. 1983. Nutrient and productivity relations of the dune grasses Ammophila arenaria and Elymus mollis. Oecologia **57**:227-232.

Peñuelas, J., J. Sardans, J. Llusia, S. M. Owen, J. Carnicer, T. W. Giambelluca, E. L. Rezende, M. Waite, and U. Niinemets. 2010. Faster returns on 'leaf economics' and different biogeochemical niche in invasive compared with native plant species. Global Change Biology **16**:2171-2185.

Perry, L., D. Blumenthal, T. Monaco, M. Paschke, and E. Redente. 2010. Immobilizing nitrogen to control plant invasion. Oecologia **163**:13-24.

Perry, L. G., S. M. Galatowitsch, and C. J. Rosen. 2004. Competitive control of invasive vegetation: a native wetland sedge suppresses Phalaris arundinacea in carbon-enriched soil. Journal of Applied Ecology **41**:151-162.

Price, J. N., and J. W. Morgan. 2007. Vegetation dynamics following resource manipulations in herb-rich woodland. Plant Ecology **188**:29-37.

Prober, S., K. Thiele, I. Lunt, and T. Koen. 2005a. Restoring ecological function in temperate grassy woodlands: manipulating soil nutrients, exotic annuals and native perennial grasses through carbon supplements and spring burns. Journal of Applied Ecology **42**:1073-1085.

Prober, S. M., K. R. Thiele, I. D. Lunt, and T. B. Koen. 2005b. Restoring ecological function in temperate grassy woodlands: Manipulating soil nutrients, exotic annuals and native perennial grasses through carbon supplements and spring burns. Journal of Applied Ecology **42**:1073-1085.

Pyšek, P., V. Jarošík, P. E. Hulme, J. Pergl, M. Hejda, U. Schaffner, and M. Vilà. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology **18**:1725-1737.

Pysek, P., K. Prach, and P. Smilauer. 1995. Relating invasion success to plant traits: an analysis of the Czech alien flora. Plant invasions: general aspects and special problems:39-60.

Pyšek, P., and D. M. Richardson. 2010. Invasive species, environmental change and management, and health. Annual Review of Environment and Resources **35**:25-55.

Reich, P. B., D. F. Grigal, J. D. Aber, and S. T. Gower. 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. Ecology **78**:335-347.

Sakai, A. K., W. L. Wagner, and L. A. Mehrhoff. 2002. Patterns of endangerment in the Hawaiian flora. Systematic Biology **51**:276-302.

Santiago-García, R. J., S. M. Colon, P. Sollins, and S. J. Van Bloem. 2008. The role of nurse trees in mitigating fire effects on tropical dry forest restoration: a case study. AMBIO: A Journal of the Human Environment **37**:604-608.

Sardans, J., M. Bartrons, O. Margalef, A. Gargallo-Garriga, I. A. Janssens, P. Ciais, M. Obersteiner, B. D. Sigurdsson, H. Y. Chen, and J. Penuelas. 2016. Plant invasion is associated with higher plant-soil nutrient concentrations in nutrient poor-environments. Global Change Biology.

Schaeffer, S., S. Billings, and R. Evans. 2003. Responses of soil nitrogen dynamics in a Mojave Desert ecosystem to manipulations in soil carbon and nitrogen availability. Oecologia **134**:547-553.

Schumacher, E., C. Kueffer, P. J. Edwards, and H. Dietz. 2009. Influence of light and nutrient conditions on seedling growth of native and invasive trees in the Seychelles. Biological Invasions **11**:1941-1954.

Scowcroft, P. G., and R. Hobdy. 1987. Recovery of goat-damaged vegetation in an insular tropical montane forest. Biotropica:208-215.

Siemann, E., J. A. Carrillo, C. A. Gabler, R. Zipp, and W. E. Rogers. 2009. Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. Forest Ecology and Management **258**:546-553.

Smith, C. W., and J. T. Tunison. 1992. Fire and alien plants in Hawaii: research and management implications for native ecosystems. Alien plant invasions in native ecosystems of Hawaii: management and research. Cooperative National Park Resources Studies Unit, Honolulu:394-408.

Spear, D., and S. L. Chown. 2009. Non-indigenous ungulates as a threat to biodiversity. Journal of Zoology **279**:1-17.

Steers, R., J. Funk, and E. Allen. 2011. Can resource-use traits predict native vs. exotic plant success in carbon amended soils? Ecological Applications **21**:1211-1224.

Suding, K., K. LeJeune, and T. Seastedt. 2004. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. Oecologia **141**:526-535.

Thaxton, J., T. Cole, S. Cordell, R. Cabin, D. Sandquist, and C. Litton. 2010. Native Species Regeneration Following Ungulate Exclusion and Nonnative Grass Removal in a Remnant Hawaiian Dry Forest. Pacific Science **64**:533-544.

Trauernicht, C., E. Pickett, C. P. Giardina, C. M. Litton, S. Cordell, and A. Beavers. 2015. The Contemporary Scale and Context of Wildfire in Hawai'i 1. Pacific Science **69**:427-444.

Van Kleunen, M., E. Weber, and M. Fischer. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology letters **13**:235-245.

Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. The American Naturalist **119**:553-572.

Vitousek, P. M. 1986. Biological invasions and ecosystem properties: can species make a difference? Pages 163-176 Ecology of biological invasions of North America and Hawaii. Springer.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Pages 183-191 Ecosystem Management. Springer.

Vitousek, P. M. 2004. Nutrient cycling and limitation: Hawai'i as a model system. Princeton University Press.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist **84**:468-478.

Vitousek, P. M., L. L. Loope, and C. P. Stone. 1987a. Introduced species in Hawaii. biological effects and opportunities for ecological research. Trends in Ecology & Evolution **2**:224-227.

Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by Myrica faya in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs **59**:247-265.

Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987b. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science **238**:802-804.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. Manual of the Flowering Plants of Hawaii. University of Hawaii Press, Honolulu.

Wedin, D. A., and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. Science **274**:1720.

Weller, S., R. Cabin, D. Lorence, S. Perlman, K. Wood, T. Flynn, and A. Sakai. 2011. Alien Plant Invasions, Introduced Ungulates, and Alternative States in a Mesic Forest in Hawaii. Restoration Ecology **19**:671-680.

Zhang, S., and Q.-L. Dang. 2006. Effects of carbon dioxide concentration and nutrition on photosynthetic functions of white birch seedlings. Tree Physiology **26**:1457-1467.

Zimmerman, N., R. Flint Hughes, S. Cordell, P. Hart, H. K. Chang, D. Perez, R. K. Like, and R. Ostertag. 2008. Patterns of primary succession of native and introduced plants in lowland wet forests in eastern Hawai ‘i. Biotropica **40**:277-284.